

Paleobiogeography of the North American Late Cretaceous Western Interior Seaway: the impact
of abiotic vs. biotic factors on macroevolutionary patterns of marine vertebrates and
invertebrates

by

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Corinne Emanuelle Myers
B.S., Cornell University, 2004
M.S., Brown University, 2008

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Chairperson: Bruce S. Lieberman

Paul Selden

Luis A. Gonzalez

Edward O. Wiley

Xingong Li

Date Defended: April 18, 2013

The Dissertation Committee for Corinne E. Myers
certifies that this is the approved version of the following dissertation:

Paleobiogeography of the North American Late Cretaceous Western Interior Seaway: the impact
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Abstract

My research investigates the relationship between ecology, evolution, and the environment in the fossil record. I hypothesize that abiotic environmental factors (e.g., climate, sea-level, ocean chemistry, and paleogeography) play a greater role in speciation, extinction, and distribution patterns than biotic factors (e.g., competition, mutualism). The effects of these factors can be observed in the fossil record as changes in species distributions, range sizes, and niche dimensions through time. Using GIS, paleoenvironmental reconstruction, and ecological niche modeling (ENM), I quantitatively investigated hypotheses of the relative influence of abiotic vs. biotic factors on macroevolution in three main studies of marine taxa from the Late Cretaceous Western Interior Seaway (WIS) of North America. The Late Cretaceous was a period of prolonged extreme and equable warmth; thus, this research has potential implications for species biology and biogeography in a projected future warmer world.

The first study examined the influence of biotic interactions on patterns of extinction by competitive exclusion in marine vertebrates. Results indicated that competitive replacement was not a mechanism mediating extinctions. Instead other factors, such as environmental changes, likely controlled extinction patterns. The second study investigated the effect of large range size on survivorship and invasion potential in marine mollusks. No relationship between large range size and extinction resistance was recovered, however, endemic species with small range sizes were more likely to become invasive. These results suggest that some biogeographic “rules” (e.g., large range size confers extinction resistance and increased invasion potential) may not prevail under conditions of prolonged and equable global warmth.

The last part of my research focused on improving methods for the application of ENM in the fossil record (paleo-ENM). In order to use ENM in the fossil record, detailed

environmental layers must be reconstructed from sedimentological and geochemical proxies. Additionally, paleo-ENM requires high-resolution stratigraphic correlations of fossil-bearing formations and collection of large species' occurrence datasets that represent the full temporal and spatial extent of the species modeled. In order to produce high fidelity models, a standardized framework for paleoenvironmental reconstruction is required. Best practices are outlined for paleoenvironmental reconstruction, in addition to the contextual framework and important considerations necessary to appropriately apply paleo-ENM.

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Chapter 1. Introduction

The over-arching goal of my research is to understand the relationship between ecology, evolution, and the environment. Specifically, my research utilizes cross-disciplinary techniques to investigate the role that biotic vs. abiotic changes play in mediating macroevolutionary patterns such as speciation, extinction, and distribution change in the fossil record. This approach integrates Earth and evolutionary history to address questions relevant to society today. 21st century environmental changes (e.g., climate warming, habitat degradation and fragmentation, changes in ocean chemistry, human-mediated introduction of new species) are projected to accelerate in our short- and long-term future. Significantly, the magnitude of biodiversity loss associated with these changes is predicted to be large enough to constitute a sixth mass extinction event, rivaling the five large mass extinctions observed in the fossil record (Leakey and Lewin 1995; McElwain and Punyasena 2007; Wake and Vredenburg 2008; Barnosky et al. 2011). While modern biological inquiry can look in detail at how species respond to these changes, biologists are limited in temporal scope; i.e., studies may span decades, but species persist for 2–10 Myrs. The Phanerozoic fossil record provides a 544-Myr history that illustrates how species have responded to similar extreme environmental changes across their lifetimes. Thus, using the fossil record, I can test in unique ways hypotheses of species' responses to some of these factors, which is informative for modern predictions and policy-making decisions (Wiens and Graham 2005; Peterson and Lieberman 2012).

Geological Setting: the Late Cretaceous Western Interior Seaway (WIS)

The Late Cretaceous WIS (Figure 1-1) is an ideal time in which to investigate the impact of biotic vs. abiotic changes on species' paleobiogeographic and macroevolutionary patterns. The WIS was a shallow (i.e., < 300 m depth) epicontinental sea connected both to the Arctic Ocean in the north and the Proto-Gulf of Mexico and Tethys Sea in the south for the 35 Myr duration of the Late Cretaceous (Hancock and Kauffman 1979; Hattin 1982; Kauffman 1984; Glancy et al. 1993; Kauffman and Caldwell 1993; Schroder-Adams et al. 1996; Kennedy et al. 1998). It is further exceptionally well-characterized both paleobiologically and geologically from over 100 years of intensive study, which minimizes the effects of systematic biases in sampling (e.g., Hancock and Kauffman 1979; Hattin 1982; Barron 1983; Kauffman 1984; Jablonski 1987; Glancy et al. 1993; Kauffman and Caldwell 1993; Schroder-Adams et al. 1996; Sageman et al. 1997; Fatherree et al. 1998; Kennedy et al. 1998; Tsujita and Westermann 1998; Poulsen et al. 2001; Huber et al. 1995, 2002; Harries 2003; Jenkyns et al. 2004; Keller et al. 2004; Cobban et al. 2006; Landman et al. 2012; Ufnar et al. 2008).

From a biotic perspective, the WIS was composed of four biotic sub-provinces (from north to south: Northern Interior sub-province, Central Interior sub-province, Southern Interior sub-province, and Gulf and Atlantic Coast sub-province) (Figure 1-1). These biotic sub-provinces (BSPs) were defined by 10-25% species endemism and are approximately analogous to modern biogeographic zones ranging from a cool temperate zone in the Northern Interior sub-province, to a subtropical zone in the southern Gulf and Atlantic coast (Kauffman 1984). Due to changing environmental conditions (e.g., sea level fluctuations), BSP boundaries in the WIS were fairly fluid providing ample opportunities for species interactions throughout the seaway.

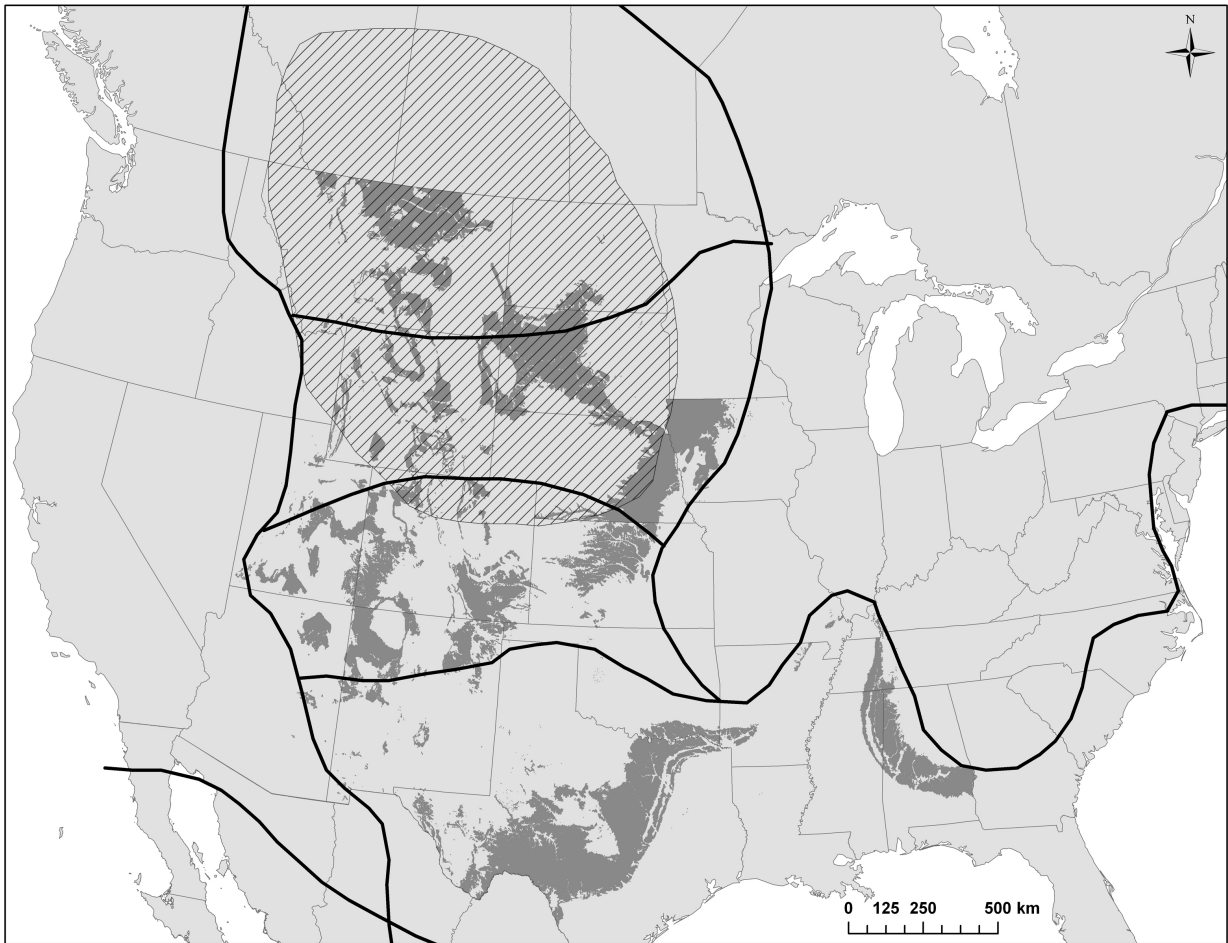


Figure 1-1. Late Cretaceous geologic outcrop record (grey). Black lines outline WIS biotic sub-province boundaries, and the WIS Endemic Center (hatched) as modified from Kauffman 1984. From north to south, biotic sub-provinces are: Northern Interior Sub-province, Central Interior Sub-province, Southern Interior Sub-province, and Gulf/Atlantic Coast Sub-province.

Periods of extreme, rapid environmental change in Earth history have the potential to be informative for making predictions about future events, and improve our general understanding of how species respond to climate extremes. Although the nature of the Late Cretaceous environment is unlikely to be a direct analogue to the climatic and oceanographic changes expected in our future, it may resemble the long-term regime into which the planet is headed (Spicer and Corfield 1992; Barron 1995; Covey et al. 1996; Haywood et al. 2011). Uniquely, the Late Cretaceous was a time of both extreme global warmth and geologically rapid environmental changes. Thus, from an abiotic perspective as well, the Late Cretaceous WIS is an excellent period to study how species interacted with a dynamic planet. Globally, Late Cretaceous climate was a “greenhouse” interval in Earth history with average annual temperatures much higher than the modern, no permanent polar ice, and a significantly reduced latitudinal thermal gradient (Barron 1983, 1995; Spicer and Corfield 1992; Covey et al. 1996; Huber et al. 1995, 2002; Jenkyns et al. 2004; Hay 2008). Moreover, the WIS experienced numerous transgressive-regressive cycles including five third-order eustatic cycles (the largest of which were the Cenomanian-Turonian Greenhorn cycle, the Coniacian-Campanian Niobrara cycle, and the Campanian-Maastrichtian Claggett/Bearpaw cycle), and several smaller fourth-order sequences (Hattin 1982; Kauffman 1984; Kauffman and Caldwell 1993). Due to the narrow connections at the northern and southern tips of the seaway, restricted marine conditions dominated, including often-brackish water conditions and a dysoxic to anoxic benthos. Normal open-marine conditions were likely short-lived (0.5-1 Myr durations) and were associated with transgressive peaks (e.g., at the Albian/Cenomanian boundary, Cenomanian/Turonian boundary, Coniacian-Santonian, and middle Campanian) (Kauffman 1984; Tsujita and Westermann 1998; Fisher and Arthur 2002).

Research Chapters and Species Database

My dissertation is composed of three main studies (two of which have been previously published in peer-reviewed journals) that investigate the impacts of biotic vs. abiotic changes on paleobiogeographic and macroevolutionary patterns of marine taxa from the Late Cretaceous WIS. Because the goal of my research is to uncover general principles of the impact of abiotic vs. biotic changes on macroevolution, the taxa included in this dissertation span a broad phylogenetic and ecological range. Both vertebrate and invertebrate taxa were investigated, including species with pelagic, nekto-benthic, and benthic adult lifestyles; ecologically, some species were dominantly predatory, some durophagous, scavengers, suspension-feeders, etc.

The full species paleobiogeographic dataset includes 83 taxa, with species' identifications vetted through direct examination by myself or one of my collaborators (Table 1-1). Geographic resolution of species occurrences is at the county level or better and stratigraphic resolution is at the level of geologic stage. In order to assign stratigraphic age to species occurrences, a stratigraphic correlation of fossil-bearing formations in the WIS across the entire 35 Myr period of the Late Cretaceous was compiled (Table 4-3 and Appendix 3). Species' paleo-range sizes were estimated using a convex hull around species' occurrence points as well as calculating latitudinal extent of species distributions during each of the six Late Cretaceous stages. ArcGIS v. 9.2 (ESRI 2006) was used to visualize and calculate range area after using the PaleoGIS extension (v. 3.0; Ross and Scotese 2000; Rothwell Group 2007) to rotate the Earth's tectonic plates to their paleo-positions during each stage. Detailed paleoenvironmental reconstructions were done based on extensive literature survey, and fieldwork conducted in South Dakota, Missouri, and Mississippi.

The first study in my dissertation tested for the effects of biotic interactions on patterns of extinction by competitive exclusion in 10 marine vertebrates (Myers and Lieberman 2011). Paleobiogeographic evidence of competitive exclusion between pairs of ecologically and phylogenetically related vertebrates was hypothesized to be shown as statistically significant negative range-area correlations through time. However, statistical evidence for such a pattern was not found, suggesting that competitive exclusion was not a mechanism mediating extinctions in these taxa. Thus other factors, such as environmental changes, were more likely controlling extinction patterns.

The second study tested for the effect of range size on patterns of survivorship and invasion potential in 63 species of WIS invertebrates (Myers et al. 2013). Counter to patterns documented by other studies, this study did not find a relationship between large range size and extinction resistance in molluscan species. Moreover, endemic species with small range sizes were more likely to become invasive. This may be a consequence of the unique conditions during the Late Cretaceous (e.g., its prolonged extreme and equable warmth). These results suggest that some biogeographic “rules” (e.g., large range size conferring extinction resistance and increased invasion potential) may not prevail under conditions of prolonged and equable global warmth.

The last study focused on the application of ecological niche modeling (ENM) in the fossil record. ENM was developed by modern biologists to estimate species’ abiotic requirements by correlating environmental factors (e.g., temperature) with known species occurrences. In the modern, spatially explicit environmental layers are easily downloadable (e.g., www.WorldClim.org; Hijmans et al. 2005). However, in the fossil record, paleoenvironmental layers must be carefully reconstructed from sedimentological and geochemical proxies. This

chapter provides guidelines and best practices for paleoenvironmental reconstruction and important conceptual considerations when applying ENM in the fossil record.

The results of these studies highlight the importance of the abiotic environment on paleobiogeographic and macroevolutionary patterns. This research illustrates that biotic interactions, such as competitive exclusion, do not seem to have a profound influence on extinction potential of marine vertebrates. Abiotic changes, however, have complex effects on species' paleobiogeography that are likely specific to the environmental regime in which species reside. ENM is a useful tool to quantify species' abiotic requirements and test specific hypotheses regarding the impact of changing environmental conditions on macroevolutionary patterns (e.g., the impact of ecological niche stability, breadth, and phylogenetic conservation on patterns of speciation, extinction, and distribution change). However, standardized methods for paleoenvironmental reconstruction and an explicit conceptual framework provide a critical foundation to producing accurate and informative models.

Table 1-1. List of marine taxa and their geologic duration in the Late Cretaceous Western Interior Seaway. Geologic stage abbreviations: Cenomanian (CEN), Turonian (TUR), Coniacian (CON), Santonian (SAN), Campanian (CAM), Maastrichtian (MAA).

Taxa	Geologic Range
Bivalvia	
<i>Agerostrea falcata</i>	CAM-MAA
<i>Anomia argentaria</i>	CAM-MAA
<i>Anomia cobbani</i>	TUR
<i>Anomia gryphorhyncus</i>	CAM-MAA
<i>Anomia micronema</i>	CAM-MAA
<i>Anomia obliqua</i>	CAM
<i>Anomia pfeiferensis</i>	TUR
<i>Anomia subquadrata</i>	TUR-CAM
<i>Crassostrea glabra</i>	CAM-MAA
<i>Exogyra columbella</i>	CEN
<i>Exogyra costata</i>	CAM-MAA
<i>Exogyra erraticostata</i>	CEN
<i>Exogyra laeviuscula</i>	SAN
<i>Exogyra levis</i>	CEN
<i>Exogyra olisiponensis</i>	CEN
<i>Exogyra tigrina</i>	SAN
<i>Exogyra triggeri</i>	CEN
<i>Ilmatogyra arietina</i>	CEN
<i>Ostrea beloiti</i>	CEN-TUR
<i>Ostrea malachitensis</i>	TUR
<i>Ostrea plumosa</i>	CAM
<i>Ostrea russelli</i>	CAM-MAA
<i>Ostrea translucida</i>	MAA
<i>Pseudoperna bentonensis</i>	TUR
<i>Pseudoperna congesta</i>	CEN-MAA
<i>Pycnodonte mutabilis</i>	CAM
<i>Pycnodonte newberryi</i>	CEN-TUR
Cephalopoda	
<i>Actinocamax manitobensis</i>	TUR-CON
<i>Actinosepia canadensis</i>	CAM-MAA
<i>Baculites aquilaensis</i>	SAN
<i>Baculites asper</i>	CON-SAN

<i>Baculites asperiformis</i>	CAM
<i>Baculites baculus</i>	CAM
<i>Baculites clinolobatus</i>	CAM
<i>Baculites codyensis</i>	CON-SAN
<i>Baculites compressus</i>	CAM
<i>Baculites compressus robinsoni</i>	CAM
<i>Baculites corrugatus</i>	CAM-MAA
<i>Baculites crickmayi</i>	CAM
<i>Baculites cuneatus</i>	CAM
<i>Baculites eliasi</i>	CAM
<i>Baculites gilberti</i>	CAM
<i>Baculites grandis</i>	CAM
<i>Baculites gregoryensis</i>	CAM
<i>Baculites haresi</i>	SAN-CAM
<i>Baculites jenseni</i>	CAM
<i>Baculites larsoni</i>	MAA
<i>Baculites maclearni</i>	CAM
<i>Baculites mariasensis</i>	TUR-CON
<i>Baculites obtusus</i>	CAM
<i>Baculites ovatus</i>	CAM-MAA
<i>Baculites perplexus</i>	CAM
<i>Baculites pseudovatus</i>	CAM
<i>Baculites undatus</i>	CAM
<i>Baculites reduncus</i>	CAM
<i>Baculites reesidei</i>	CAM
<i>Baculites rugosus</i>	CAM
<i>Baculites scotti</i>	CAM
<i>Baculites</i> sp. (smooth spp.)	CAM
<i>Baculites</i> sp. (smooth)	CAM
<i>Baculites</i> sp. (weak flank ribs)	CAM
<i>Baculites sweetgrassensis</i>	CON
<i>Baculites taylorensis</i>	CAM
<i>Baculites texanus</i>	CAM
<i>Baculites thomi</i>	CON-CAM
<i>Baculites undulatus</i>	TUR
<i>Baculites yokoyamai</i>	CEN-CON, CAM
<i>Belemnitella bulbosa</i>	MAA
<i>Eubaculites carinatus</i>	MAA

<i>Eutrephoceras alcesence</i>	CAM
<i>Eutrephoceras dekayi</i>	CAM-MAA
<i>Pseudobaculites natosini</i>	CAM-MAA
<i>Pseudobaculites nodosus</i>	CON
<i>Pseudobaculites wyomingensis</i>	CON
<i>Sciponoceras gracilis</i>	CEN-TUR
<i>Trachybaculites columna</i>	MAA
<i>Tusoteuthis longa</i>	CAM
Gastropoda	
<i>Anisomyon apicalis</i>	TUR-CON
<i>Anisomyon borealis</i>	CAM-MAA
<i>Anisomyon centrale</i>	CAM-MAA
<i>Drepanochilus evansi</i>	CAM-MAA
<i>Euspira obliqua</i>	MAA
<i>Euspira rectilabrum</i>	CAM-MAA
<i>Graphidula culbertsoni</i>	MAA
<i>Turritella vertebroides</i>	CAM
<i>Turritella whitei</i>	CEN
Maxillopoda	
<i>Stramentum elegans</i>	TUR
Reptilia	
<i>Tylosaurus</i> sp.	CON-MAA
<i>Platecarpus</i> sp.	CON-CAM
Actinopterygii	
<i>Xiphacinus</i> sp.	CEN-MAA
Chondrichthyes	
<i>Cretoxyrhina mantelli</i>	CEN-SAN
<i>Squalicorax falcatus</i>	CEN-CAM
<i>Squalicorax kaupi</i>	CON-MAA
<i>Ptychodus anonymous</i>	CEN-CON
<i>Ptychodus mortoni</i>	TUR-CAM
<i>Ptychodus whipplei</i>	CEN-CON
<i>Rhinobatos incertus</i>	CEN-CAM

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Chapter 2. Sharks That Pass In The Night: Using GIS to Investigate Competition in the Cretaceous Western Interior Seaway

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Abstract

One way the effects of both ecology and environment on species can be observed in the fossil record is as changes in geographic distribution and range size. The prevalence of competitive interactions and species replacements in the fossil record has long been investigated and many evolutionary perspectives, including those of Darwin, have emphasized the importance of competitive interactions that ultimately lead one species to replace another. However, evidence for such phenomena in the fossil record is not always manifest. Here we use new quantitative analytical techniques based on geographic information systems (GIS) and PaleoGIS tectonic reconstructions to consider this issue in greater detail. The abundant, well-preserved fossil marine vertebrates of the Late Cretaceous Western Interior Seaway of North America provide the component data for this study. Statistical analysis of distributional and range size changes in taxa confirms earlier ideas that the relative frequency of competitive replacement in the fossil record is limited to non-existent. It appears that typically environmental gradients played the primary role in determining species distributions, with competitive interactions playing a more minor role.

Introduction

Historical Perspective

A central question in biogeography and evolution is what causes species' distributions to wax and wane through time. Traditionally, a dominant role has been ascribed to competitive interactions between species (Darwin 1859, MacArthur and Wilson 1972, Van Valen, 1987, Vermeij 1987, Jackson and McKinney 1990, Rosenzweig and McCord 1991, Sepkoski *et al.* 2000). Classic examples include the decline and replacement of brachiopods by bivalves, mammal-like reptiles by archosaurs, cyclostome bryozoans by cheilostome bryozoans, gymnosperms by angiosperms, multituberculates by rodents, and South American mammals by North American fauna; however, these cases for the most part have not been tested in detail (Benton 1987, 1996a, Rayner and Masters 1995). The theoretical importance of competition in evolution actually pre-dates Darwinian competitively driven natural selection and can be traced back to the notion of plenitude. Plenitude ascribes a fixed number of ecological niches on Earth, with rapid evolution of life to fill all available niche space. Once filled, evolution occurs in dynamic equilibrium where individual species may arise and go extinct, but patterns of global diversity remain constant (Cifelli 1981, Walker and Valentine 1984, Benton 1987, 1996b). Darwin (1859) supported this view, particularly with his famous wedge analogy, where species are akin to wedges hammered into a surface – once the surface is filled with wedges, a new wedge may only be driven in at the expense of an older wedge being driven out (Gould and Calloway 1980, Gould 1985, Benton 1996b). From this perspective, evolution occurs by a series of competitive replacements through time, species' distributions are predominantly controlled by competitive interactions with contemporaries, and interspecific competition is a primary driver of macroevolution.

An alternative perspective is where an existing species or clade is successful until an external perturbation results in its extinction and later replacement by a new taxon. For instance, a re-examination of the diversity patterns of brachiopods and bivalves by Gould and Calloway found these clades to be as “ships that pass in the night” (Longfellow, IN: Gould and Calloway 1980); a view in accord with the notion that abiotic environmental change dictates species origination and extinction patterns (Eldredge and Cracraft 1980, Vrba 1980, 1985, Cifelli 1981, Gould 1985, Masters and Rayner 1993, Benton 1996a, 2009, Barnosky 2001, Flagstad *et al.* 2001, Lieberman *et al.* 2007).

Of course these (and other) authors acknowledge that both factors likely play some role in evolution. Thus, here we test for evidence of interspecific competition on species’ distributions over macroevolutionary timescales by concentrating on identification of competitive replacements in fossil taxa using GIS. GIS-based techniques are increasingly recognized as powerful tools for investigating evolutionary patterns and processes (Rode and Lieberman 2004, Stigall and Lieberman 2006, Costa *et al.* 2008, Kozak *et al.* 2008, Butler *et al.* 2010). These methods allow for quantitative measurement of distribution and range size change during specific temporal intervals. Further, GIS analyses lend themselves to statistical analysis of negative range area correlations in species pairs through time, which can be used as a proxy for evidence of competitive replacement. The focus of this analysis is a set of marine vertebrate species from the exceptionally diverse and complete record of the Late Cretaceous Western Interior Seaway of North America. This region has been the subject of palaeobiological and geological study for more than a century and has been intensely sampled. Further, palaeobiological samples can be placed in a detailed stratigraphic context.

Geological Setting

The Late Cretaceous covers a 35 million year period between 100-65Ma. The Earth at this time was in a greenhouse climate state with little or no polar ice (Barron 1983, Huber *et al.* 2002, Spicer 2002, Everhart 2005). As a consequence of this, and higher rates of sea floor spreading, sea-level was much higher than today. In particular, central North America was covered by a shallow epicontinental sea, the Western Interior Seaway (WIS) (i.e. $\leq 600\text{m}$ water depth) (Hattin 1982, Kauffman and Caldwell 1993, Poulsen *et al.* 2001, Everhart 2005). The WIS represents a foreland basin formed by tectonic loading and lithospheric flexure during uplift of the Rocky Mountains to the west. This basin was inundated episodically from both boreal waters extending south from the Arctic Ocean and tropical waters extending north from the proto-Atlantic/Tethys seas (Hattin 1982, Kauffman 1984, Kauffman and Caldwell 1993, Shimada *et al.* 2006). At the end of the Early Cretaceous (late Albian, $\sim 100\text{Ma}$) a global sea-level low stand separated the northern and southern arms of the WIS for the last time until the late Maastrichtian ($\sim 65\text{Ma}$). Cyclic sea-level changes are recorded in the WIS as three major transgressive/regressive events: the Greenhorn Cycle (late Cenomanian-Turonian), which included the sea-level high stand for the Late Cretaceous with eustatic sea-levels upwards of 250m higher than today; the Niobrara Cycle (late Coniacian – early Campanian); and the Claggett/Bearpaw Cycle (Campanian – Maastrichtian) (Hattin 1982, Kauffman 1984, Kauffman and Caldwell 1993).

Our understanding of the Late Cretaceous WIS is based on over one hundred years of field and laboratory work by geologists, palaeoclimatologists, and palaeobiologists. As a consequence, the tectonic, environmental, and geologic history of this area is well understood and extensively palaeobiologically sampled making it an ideal region for this type of

palaeobiogeographical investigation (e.g., Hancock and Kauffman 1979, Hattin 1982, Kauffman 1984, Nicholls & Russell 1990, Glancy *et al.* 1993, Russell 1993, Schroder-Adams *et al.* 1996, Sageman *et al.* 1997, Schwimmer *et al.* 1997, Keller *et al.* 2004, Everhart 2001, 2005, Becker *et al.* 2006, Cobban *et al.* 2006, Shimada *et al.* 2006, Ufnar *et al.* 2008). However, extensive sampling does not always equate to representative sampling; consequently, we provide various tests to assess the quality of the WIS record and its use in palaeobiogeographical analyses.

Materials and Methods

Data Collection

A temporal and geographic occurrence database was generated for ten Late Cretaceous WIS vertebrate taxa. Taxa included four genera of shark: three species of *Ptychodus* (*P. anonymus*, *P. mortoni*, and *P. whipplei*), one species of *Cretoxyrhina* (*C. mantelli*), two species of *Squalicorax* (*S. falcatus* and *S. kaupi*) and one species of *Rhinobatos* (*Rhinobatos incertus*); as well as two genera of mosasaur (*Platecarpus* sp., and *Tylosaurus* sp.) and one teleost genus (*Xiphactinus* sp.). The taxa included in this analysis were chosen because they are common and abundant in the WIS fossil record, persist through at least three geologic stages of the Late Cretaceous, and have been well characterized taxonomically and palaeobiologically. Further, the WIS at this time had no prominent physical barriers that might have prevented interactions between taxa.

Data on species' geographic and stratigraphic ranges were collected through examination of museum collections, fieldwork, and survey of the literature. The following museum collections were used: Natural History Museum and Biodiversity Research Center (NHM-BI, University of Kansas); Peabody Museum of Natural History (YPM, Yale University); Texas

Memorial Museum (TMM, University of Texas – Austin); Sternberg Museum of Natural History (FHSM, Fort Hays State University); University of Colorado Museum (UCB, University of Colorado – Boulder); University of Nebraska State Museum (UNSM); and the Black Hills Institute (BHI, South Dakota). These museums contain important and diverse collections of WIS taxa spanning the majority of Late Cretaceous WIS geography, and taxa in these collections are well-documented geographically and stratigraphically. All museum specimens were personally examined and identification confirmed by the authors. In cases where species identifications lacked confidence, analyses were run at the generic level (e.g. *Tylosaurus*, *Platecarpus*, *Xiphactinus*). To augment information from museums, fieldwork was conducted at Late Cretaceous sites in western South Dakota and southeastern Missouri.

Resolution of geographic locality data was at the county-level and better, the standard level of resolution used in other GIS-based palaeobiogeographic analyses (e.g., Rode and Lieberman 2004, Hendricks *et al.* 2008, Maguire and Stigall 2009). However, most data represent even higher resolution at the 1 mi² township, range, and section. Temporal resolution was at the level of geologic stage within the Late Cretaceous and characterized by formation and member of specimen occurrence. The resulting database consists of 762 total occurrence points; the number of occurrence points per taxon (species and in some cases genus) varies from 31 to 197 (Figure 2-1, Appendix 1-1).

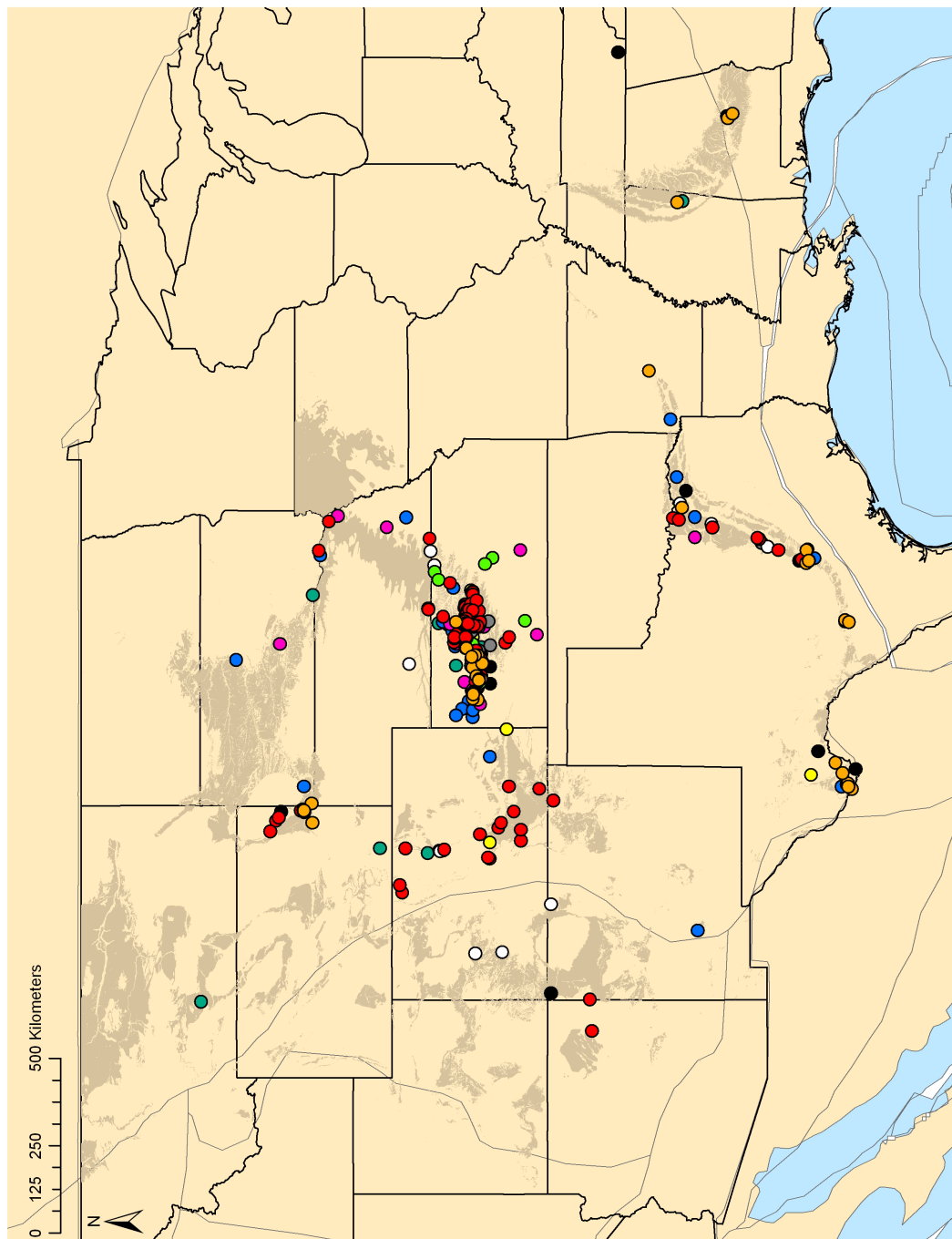


Figure 2-1. Data points showing occurrence records of Late Cretaceous marine vertebrate specimens analyzed in this study. *Xiphactinus* sp. (pink), *Platecarpus* sp. (dark green), *Tylosaurus* sp. (dark blue), *Squalicorax kaupi* (orange), *Squalicorax falcatus* (red), *Rhinobatos incertus* (light green), *Ptychodus whipplei* (white), *Ptychodus mortoni* (dark gray), *Ptychodus anonymus* (light gray), *Cretoxyrhina mantelli* (yellow). Present day outcrop of Late Cretaceous sediments is also shown (brown).

Range Reconstructions

Geographic locality data for each species' occurrence was georeferenced and imported into ArcGIS v.9.2 for visual representation and spatial analysis (ESRI 2006). PaleoGIS v.3.0 (Scotese 1998, Ross and Scotese 2000, Rothwell Group 2007) was then used to reconstruct the palaeogeography of each stage during the Late Cretaceous following the methods of Rode and Lieberman (2004) and Stigall and Lieberman (2006) (Figure 2-2). This step ensures that distribution and range area reconstructions minimize estimation error due to tectonic contraction and expansion in the North American plate over the course of the Late Cretaceous.

Once PaleoGIS was used to reconstruct the geography of a particular stage, a ten kilometer buffer was applied to each specimen occurrence point. Buffering species' locality points helps control for any error in the translation from current geographic location to deep time georeferenced latitude and longitude. Additionally, buffering gives area to point occurrence data, enabling retention of these data in the analysis. ArcGIS was then used to construct least-fit polygons for each taxon at each temporal interval. The spatial analysis software available within this program was used to calculate area of each reconstructed range. Geographic range data for all taxa are provided in Appendix 1-1.

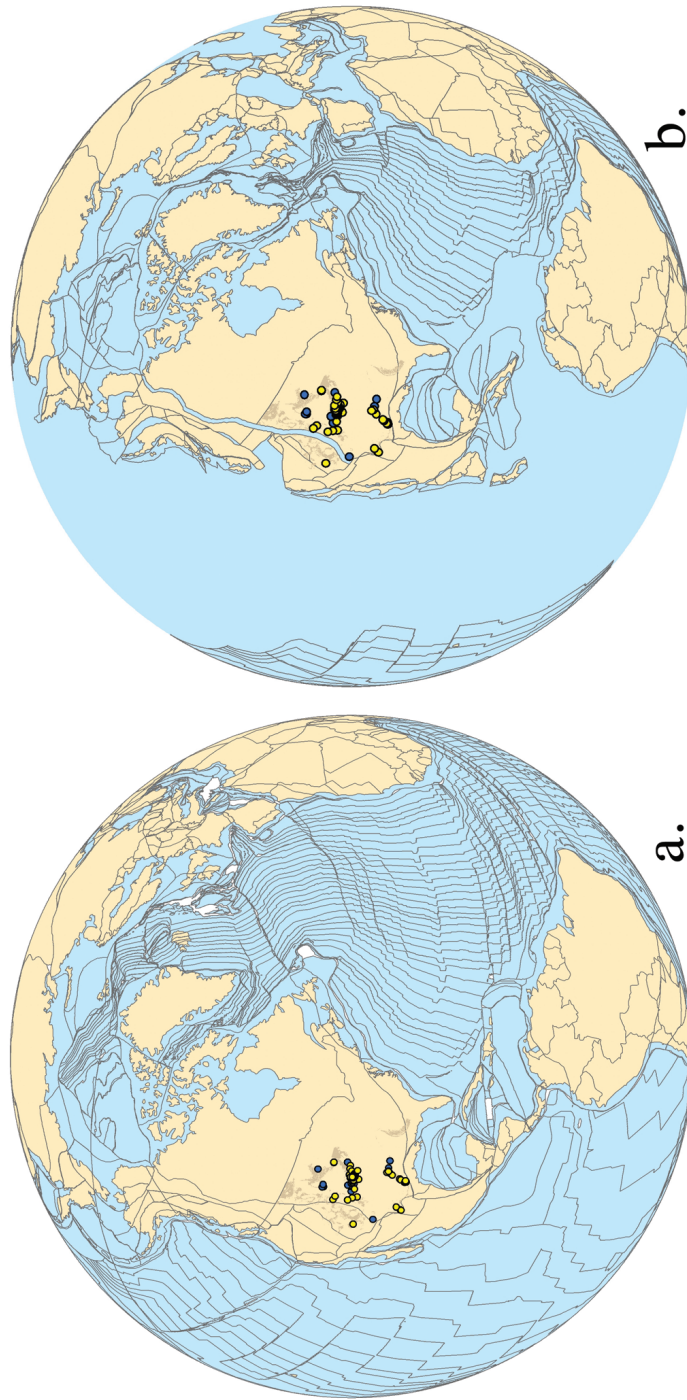


Figure 2-2. Example of PaleogeGIS (Rothwell Group 2007) plate tectonic reconstruction. Distribution of *Cretoxyrhina mantelli* (yellow), *Tylosaurus* sp. (blue). Present day outcrop of Late Cretaceous sediments is also shown (brown). (a) PaleogeGIS present day tectonic configuration. (b) PaleogeGIS Coniacian reconstruction (~87Ma).

Identifying Competition

One way competition can be observed in the fossil record is as changes in species' distribution and range size through time. Benton (1996a, b) defined "Candidate Competitive Replacements" (CCRs) as species pairs showing negatively correlated abundance and diversity patterns over time. CCRs must involve taxa with overlapping geographic and stratigraphic ranges and should also involve comparisons between taxa with similar habitat, body size, and diet. Further, all CCRs must show a distinctly "successful" taxon (the survivor) as well as a distinctly "unsuccessful" taxon, identified by range contraction and extinction within two temporal intervals after the minimum date of origin of the "successful" taxon (Benton 1996a, b). This pattern can also be identified in the fossil record as negatively correlated geographic range area through time, which can be tested for statistical significance using nonparametric rank correlation in PAST v.2.01 (Hammer *et al.* 2001) (Spearman's ρ and Kendall's τ , $p \leq 0.05$); these statistical analyses were corrected for multiple comparisons using the Bonferroni correction.

All taxa under investigation display geographic and stratigraphic overlap. To identify CCRs, taxa with similar inferred ecotypes were compared, as taxa within the same ecotype are most likely to have interacted competitively. The taxa in this study can be divided into two general palaeoecologies: species of *Cretoxyrhina*, *Squalicorax*, *Tylosaurus*, *Platecarpus*, and *Xiphactinus* are inferred to have been pelagic predators (e.g., Russell 1967, Williamson *et al.* 1993, Everhart 2005, Rothschild *et al.* 2005, Shimada and Cicimurri 2005, Becker 2006, Shimada *et al.* 2006; see Schwimmer *et al.* 1997 for additional discussions of *Squalicorax*); species of *Ptychodus* and *Rhinobatos* are inferred to have had a nekto-benthic, durophagous lifestyle (e.g., Stewart 1988, Williamson *et al.* 1993, Everhart 2005, 2007, Shimada *et al.* 2006;

see Hamm 2008, 2010 for additional discussions of *Ptychodus*). Comparisons were also conducted by genus, as species within the same genus may be more likely to have the greatest degree of competitive overlap. Finally, an agnostic approach was used, and pairwise comparisons between all taxa were considered.

Analysis of Bias

There are many phenomena that can explain why one species range might increase through time while another decreases through time. In addition to competition and other processes discussed below, an incomplete fossil record could artificially produce a pattern mirroring a CCR. Incompleteness of the fossil record is a potential source of bias in any palaeontological study. As previously mentioned, the Late Cretaceous WIS has been exhaustively studied for over a century and is well characterized both in terms of its geology and palaeontology. Further, it has not undergone significant tectonic modification since the Late Cretaceous. These may all partly serve to obviate the potential problems of an incomplete fossil record. Moreover, some areas within the WIS show exceptional preservation in the form of Konservat Lagerstätte; one of these, the Smoky Hill Chalk member of the Niobrara Formation spans three temporal intervals (Coniacian, Santonian, and Campanian stages) of this study (Schwimmer *et al.* 1997, Meyer and Milsom 2001, Bottjer 2002).

However, this does not mean that there might not be certain taphonomic factors conspiring to cloud our understanding of biogeographic patterns in these taxa over time. Because of this, three tests were used to determine if incompleteness or bias in the WIS fossil record is artifactually influencing palaeobiogeographic patterns, including those pertaining to CCRs. First, the robustness of range area reconstructions to potential outliers was tested by resampling occurrence points for each taxon. An ‘n-1’ jackknifing procedure was utilized to estimate the

resampled mean range size and associated confidence bands for each taxon during each time interval (resampled data available in Appendix 1-1). Mean range area was then subjected to nonparametric rank correlation tests and the results were compared to those obtained using original range area calculations (tests on resampled data available in Appendix 1-3 and 1-4, and discussed more fully below).

The second test compared geographic range size in each taxon to area of available Late Cretaceous sedimentary outcrop. A high percentage of overlap between the distribution of taxa and available outcrop would suggest that presence/absence of Late Cretaceous geologic record may be influencing our results. The third test aimed to identify a correlation between number of data points and geographic range size for each temporal interval. In this case, if sampling bias had an effect on our range size reconstructions, a strong positive correlation between number of data points and range size would be expected.

Results

Competition in the WIS

Tables 2-1 and 2-2 show the results of intrageneric range area correlations and correlations by palaeoecotypes respectively; pairwise comparisons between all taxa are included in Appendix 1-2. All species did show changes in distribution and range size through time. The majority of the species comparisons showed no evidence of interspecific competition (e.g., Figure 2-3). A complete set of geographic comparisons for all taxa considered is provided in Appendix 1-5 to 1-47). Some taxa did generally show the basic biogeographic pattern predicted for a CCR (Figure 2-4), however, when analyzed the pattern was not found to be statistically significant. Indeed, no statistically significant negative range area correlations were identified

from intrageneric comparisons, within ecotype comparisons, or when all taxa were compared, after the Bonferroni correction was applied. For instance, consider that among the four possible intrageneric comparisons, only *Squalicorax falcatus* and *S. kaupi* is near significance using Kendall's τ ($\tau = -0.69007$, $p = 0.0518$), but the correlation is not significant after a Bonferroni correction for multiple comparisons was applied (new critical p-value of $p \leq 0.013$) (Table 2-1). Thus, it appears that for these vertebrate taxa evidence for candidate competitive replacements in the Cretaceous WIS is negligible to non-existent.

Table 2-1. Intrageneric range area correlations. A Bonferroni correction (Sokal and Rohlf 1995)

for multiple comparisons indicates a critical p-value of $p \leq 0.013$ for statistical significance.

Taxon A	Taxon B	Spearman's ρ	p-value	Kendall's τ	p-value
<i>Squalicorax falcatus</i>	<i>Squalicorax kaupi</i>	-0.812	0.072	-0.690	0.052
<i>Ptychodus anonymus</i>	<i>Ptychodus mortoni</i>	-0.185	0.742	-0.077	0.828
<i>Ptychodus anonymus</i>	<i>Ptychodus whipplei</i>	0.936	0.025	0.833	0.019
<i>Ptychodus mortoni</i>	<i>Ptychodus whipplei</i>	0.092	0.883	0.077	0.828

Table 2-2. Range area correlations among species with similar palaeoecology. (a) Inferred large, pelagic (circular vertebral centra suggesting fusiform-body) predators; (b) inferred large, nekto-benthic durophagous lifestyle. A Bonferroni correction (Sokal and Rohlf 1995) for multiple comparisons indicates a critical p-value of $p \leq 0.002$ for statistical significance.

Taxon A	Taxon B	Spearman's ρ	p-value	Kendall's τ	p-value
(a) Inferred pelagic, predatory taxa					
<i>Cretoxyrhina mantelli</i>	<i>Squalicorax falcatus</i>	0.928	0.022	0.828	0.020
<i>Cretoxyrhina mantelli</i>	<i>Squalicorax kaupi</i>	-0.882	0.036	-0.786	0.027
<i>Cretoxyrhina mantelli</i>	<i>Tylosaurus</i> sp.	-0.765	0.097	-0.643	0.070
<i>Cretoxyrhina mantelli</i>	<i>Platecarpus</i> sp.	-0.431	0.392	-0.386	0.277
<i>Cretoxyrhina mantelli</i>	<i>Xiphactinus</i> sp.	0.174	0.733	0.138	0.697
<i>Squalicorax falcatus</i>	<i>Squalicorax kaupi</i>	-0.812	0.072	-0.690	0.052
<i>Squalicorax falcatus</i>	<i>Tylosaurus</i> sp.	-0.696	0.144	-0.552	0.120
<i>Squalicorax falcatus</i>	<i>Platecarpus</i> sp.	-0.334	0.533	-0.298	0.401
<i>Squalicorax falcatus</i>	<i>Xiphactinus</i> sp.	0.371	0.419	0.333	0.348
<i>Squalicorax kaupi</i>	<i>Tylosaurus</i> sp.	0.765	0.097	0.571	0.107
<i>Squalicorax kaupi</i>	<i>Platecarpus</i> sp.	0.770	0.108	0.617	0.082
<i>Squalicorax kaupi</i>	<i>Xiphactinus</i> sp.	0.058	0.933	0.000	1.000
<i>Platecarpus</i> sp.	<i>Tylosaurus</i> sp.	0.524	0.283	0.463	0.192
<i>Platecarpus</i> sp.	<i>Xiphactinus</i> sp.	0.152	0.833	0.149	0.674
<i>Tylosaurus</i> sp.	<i>Xiphactinus</i> sp.	-0.058	0.933	-0.138	0.697
(b) Inferred nekto-benthic, durophagous taxa					
<i>Ptychodus anonymus</i>	<i>Ptychodus mortoni</i>	-0.185	0.7417	-0.0772	0.828
<i>Ptychodus anonymus</i>	<i>Ptychodus whipplei</i>	0.936	0.0250	0.8333	0.019
<i>Ptychodus anonymus</i>	<i>Rhinobatos incertus</i>	0.880	0.0500	0.7454	0.036
<i>Ptychodus mortoni</i>	<i>Ptychodus whipplei</i>	0.092	0.8833	0.0772	0.828
<i>Ptychodus mortoni</i>	<i>Rhinobatos incertus</i>	-0.058	0.9333	0.0000	1.000
<i>Ptychodus whipplei</i>	<i>Rhinobatos incertus</i>	0.7860	0.1167	0.5963	0.093

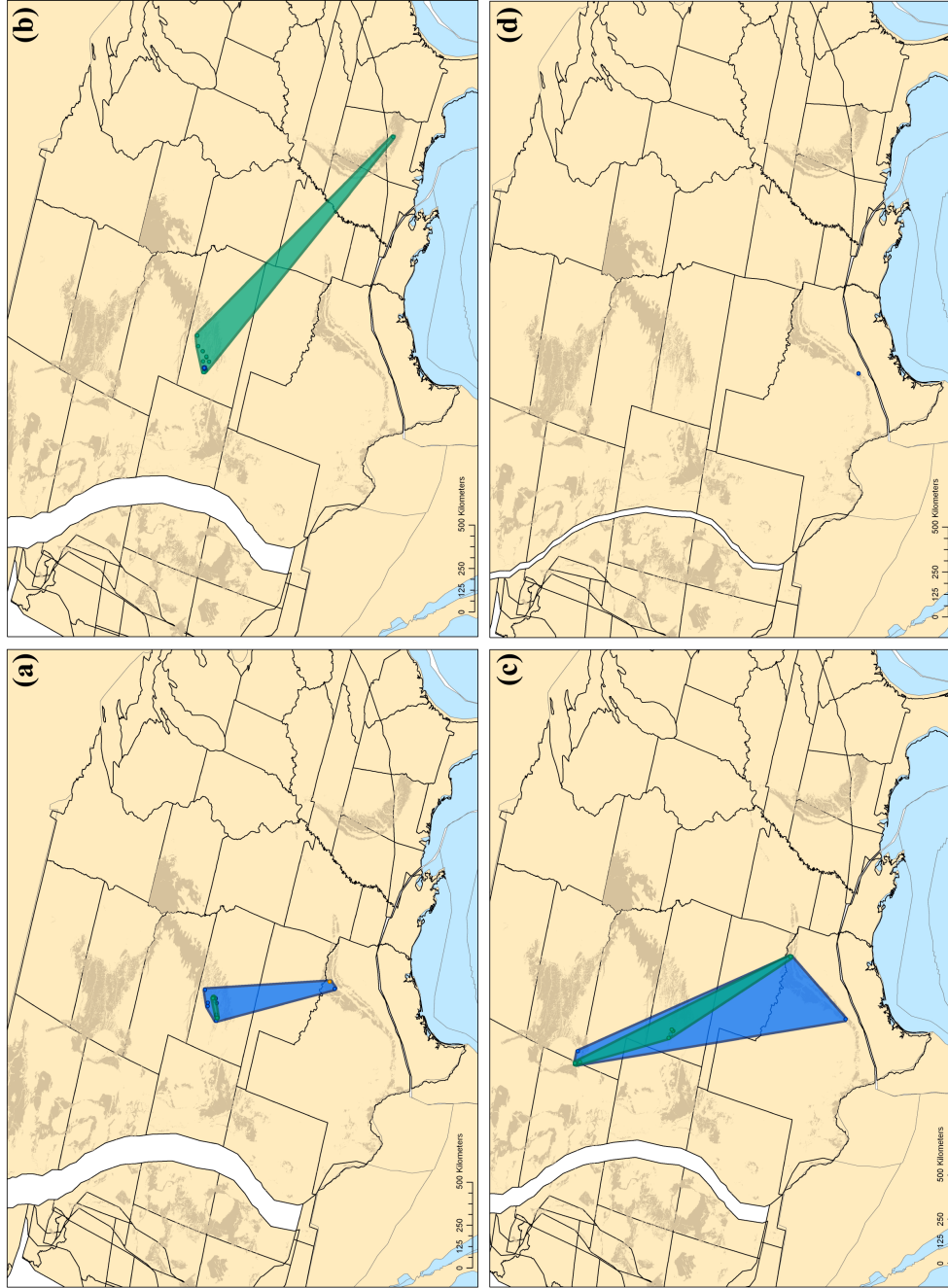


Figure 2-3. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the paleobiogeographic patterns uncovered for the majority of two-taxon comparisons in this study. *Tylotaurus* sp. (blue) and *Platecarpus* sp. (dark green) distributions are shown during the Late Cretaceous. Late Cretaceous stages: (a) Coniacian, (b) Santonian, (c) Campanian, (d) Maastrichtian. These taxa do not show a statistically significant negative range area correlation through time and thus are not identified as CCRs. Present day outcrop of Late Cretaceous sediments is also shown (brown).

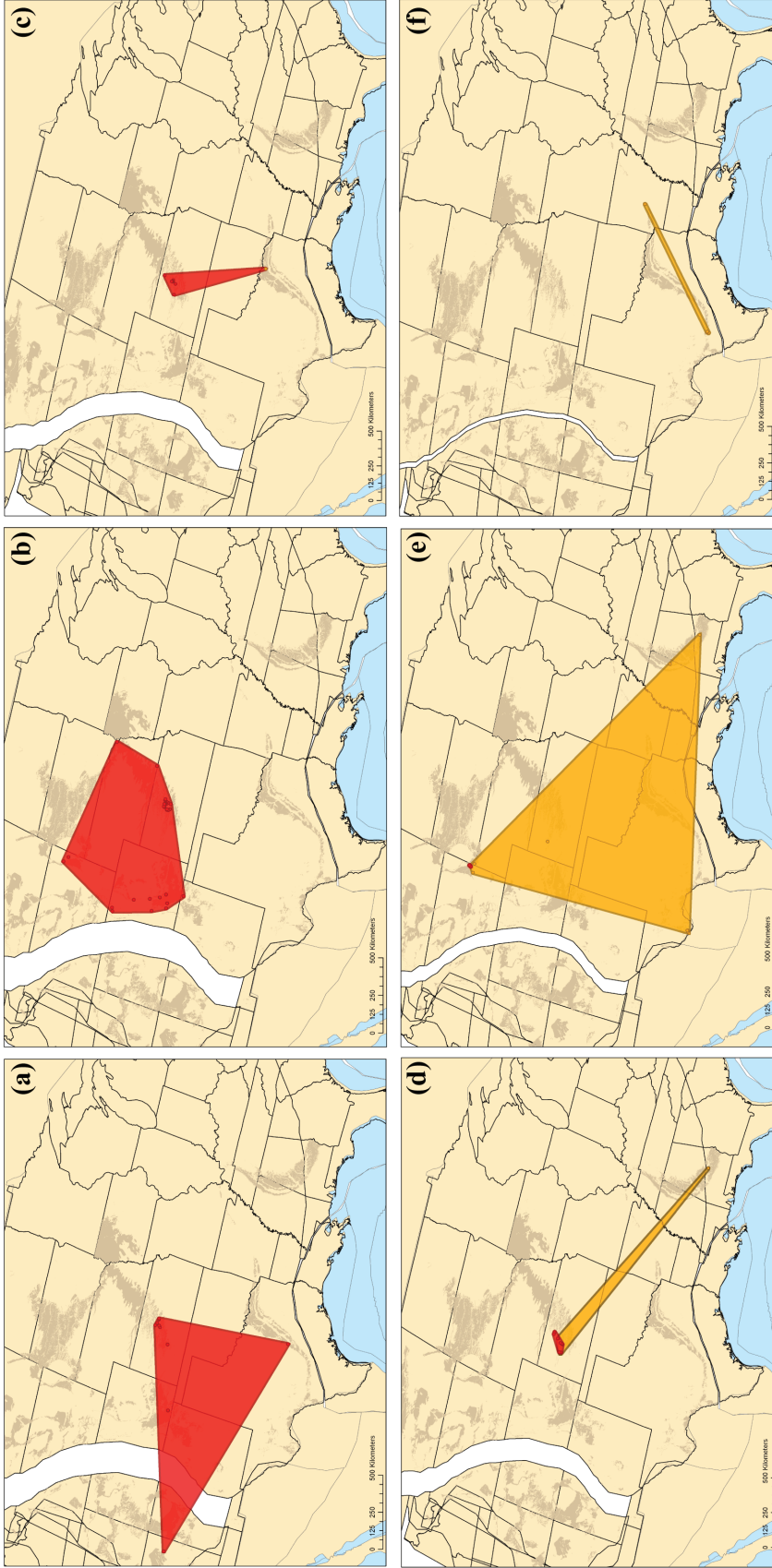


Figure 2-4. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the general predicted geographic pattern of a CCR, although the negative relationship in range size is not statistically significant. *Squalicorax falcatus* (red), and *S. kaupi* (orange) distributions are shown during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. *S. falcatus* shows stable, though dynamic, range size until the origination of *S. kaupi* in the Coniacian (c). After this time, *S. falcatus* experiences sequential decrease in range size resulting in extinction at the end Campanian (e). This example illustrates a negative relationship between the range area of two ecologically similar species within the same genus, and thus could represent a competitive replacement of *S. falcatus* by *S. kaupi*. Present day outcrop of Late Cretaceous sediments is also shown (brown).

Analysis of Bias

Geographic range estimations using this palaeobiogeographic method may be susceptible to artificial inflation by widely flung single occurrence points. In order to assess the influence of these potential outliers on our range reconstructions, and thus pertaining to the identification of statistically significant CCRs, we re-ran all the pairwise comparisons using the estimated mean geographic range calculated by jackknifing (Appendix 1-3). The results are identical: before or after correcting for multiple comparisons, no statistically significant intrageneric or within ecotype CCRs were identified; when all taxa were compared, two CCRs only appeared statistically significant before the Bonferroni correction was applied: they were no longer significant after correction for multiple comparisons. Thus, the results from analysis of the original data and the resampled data are equivalent and the data appear robust to resampling. Consequently, outliers are not likely to be playing a significant role in influencing the results.

To test for the effect of available outcrop area on species distributions during the Late Cretaceous, we compared species' geographic range size with area of Late Cretaceous sedimentary record; the approximate margins of the WIS for the early, middle, and late Late Cretaceous, along with the occurrence records parsed by stage, are shown in Appendix 1-48. Taxa were shown to occupy only 4–37% of potential habitat. Because taxa are not present in all or even the majority of available outcrop area during this time period, it is unlikely that the simple availability of Late Cretaceous sedimentary record is controlling the patterns of distribution and range size change observed in this analysis.

A correlation of number of unique geographic localities sampled with size of geographic range reconstruction for each temporal interval in this analysis is shown in Table 2-3 (for correlation statistics using resampled means, see Appendix 1-4). The number of unique localities

was used to test for sampling bias (instead of all sampled occurrences) because this reduces artificial inflation of points sampled and maximizes the potential for finding a significant correlation (thus the test is most sensitive to identifying sampling bias). None of the stages during the Late Cretaceous show significant correlations between number of data points and size of geographic range ($p \gg 0.007$ using Bonferroni correction for multiple comparisons) except the Coniacian stage ($p = 0.001$) (Table 2-3); the same is true of the resampled data (Appendix 1-4).

Many (though not all) taxa have small geographic range size during the Coniacian; it is possible that this represents a bias in collection or preservation. On the other hand, this stage is the point of origin or extinction for a number of the taxa studied (e.g., *Tylosaurus* sp., *Platecarpus* sp., *Squalicorax kaupi* originate; *Ptychodus anonymus* and *Ptychodus whipplei* go extinct). Species commonly have small geographic range size at the point of origination and extinction (particularly if speciation occurs allopatrically in small isolated populations and extinction first involves reduction to a single population). To assess the influence of this phenomenon, these taxa were removed and the correlation statistics re-run (Table 2-3, and Appendix 1-4). Excluding taxa originating or going extinct, the number of sampled localities during the Coniacian is no longer significantly correlated with reconstructed range size in both the original and the resampled data (see Table 2-3 and Appendix 1-4). Thus the uniquely small range size of these taxa was likely causing the suggested sampling bias during this interval.

Table 2-3. Correlation results between number of unique geographic localities sampled and reconstructed geographic range size for each stage during the Late Cretaceous. A Bonferroni correction (Sokal and Rohlf 1995) for multiple comparisons indicates a critical p-value of $p \leq 0.007$ for statistical significance. Coniacian* represents correlation between number of unique geographic localities and reconstructed range size after removing taxa that either originate or go extinct during this stage.

Stage	Spearman's ρ	p-value	Kendall's τ	p-value
Cenomanian	0.886	0.016	0.733	0.039
Turonian	0.775	0.049	0.683	0.031
Coniacian	0.905	0.001	0.805	0.001
Coniacian*	0.700	0.2333	0.600	0.142
Santonian	0.551	0.163	0.743	0.101
Campanian	0.764	0.056	0.651	0.040
Maastrichtian	0.886	0.667	0.817	0.201
Total (combined)	0.733	0.020	0.556	0.025

Discussion

This study uses new techniques in quantitative biogeographic analysis to test for the role of competitive replacement in the fossil record. We focused on species' distributions in the abundant representatives of the vertebrate fauna from the Late Cretaceous WIS, specifically looking for two-taxon comparisons suggesting competitive replacement. No two-taxon comparisons showed any statistical evidence of significant, negative geographic range correlations. These results reiterate previous analyses indicating little evidence for competitive replacement (Benton 1996a, b). Further, this suggests that something other than interspecific competition plays the predominant role in influencing species distributions over macroevolutionary time scales. Such processes were most likely abiotic environmental changes, both climatic and tectonic, as these have been shown to have had a significant impact on species distributions and macroevolution at other times in the history of life (Lieberman and Eldredge 1996, Lieberman 2000, Barnosky 2001, Flagstad *et al.* 2001, Rode and Lieberman 2004, Stigall and Lieberman 2006, Hendricks *et al.* 2008, Benton 2009, Gates *et al.* 2010). There could, however, also be a substantial contribution from ecological factors such as food source tracking, intraspecific interactions, etc.

It is worth noting that competitive replacement may be more prevalent among species that are rare and/or geographically restricted. Such cases are difficult to identify in the fossil record, and thus by necessity our study focused on more abundant and potentially more “successful” taxa from the outset. As a consequence, even though we attempted to maximize recovery of CCRs by using broad definitions of palaeoecological similarity, our estimate of the frequency of CCRs is most surely an underestimate. Nonetheless, it is based on quantitative and detailed investigation of these groups, and thus the best estimate possible at present.

Moreover, while we believe that our analysis includes real species using a phylogenetic species concept, it is impossible to exclude the possibility that some of these species actually represent ecomorphs within a single lineage. If this were the case, then instead of identifying cases of competitive replacement between species, our analysis would be testing for intraspecific interactions occurring between co-occurring ecomorphs. The apparent non-prevalence of competitive replacement within potentially adaptive lineages then might suggest that ecomorph evolution also may not be strongly influenced by these types of competitive interactions.

Ultimately, this study provides little evidence that CCRs play a defining role in shaping species' distributions at the macroevolutionary scale. The driving force is instead likely to be abiotic environmental factors, such as climate and sea-level changes, that determine species distribution and range size. Other ecological factors may have been important as well, but interspecific competition does not appear to have had a major affect on macroevolutionary patterns of species in the fossil record (Vrba 1980, Nicholls & Russell 1990, Barnosky 2001, Flagstad *et al.* 2001, Benton 2009, Gates *et al.* 2010, Venditti *et al.* 2010).

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Chapter 3. Greenhouse biogeography: the relationship of geographic range to invasion and extinction in the Cretaceous Western Interior Seaway

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Abstract

Significant warming of the Earth's climate in the near-term seems increasingly likely. If significant enough, in the long-term this climatic regime could come to resemble previous greenhouse intervals in Earth history. Consequently, analysis of the fossil record during periods of extreme warmth may provide important lessons for species biology, including biogeography, in a much warmer world. To explore this issue, we analyzed the biogeographic response of 63 molluscan species to the long-term global warmth in the Late Cretaceous Western Interior Seaway (WIS) of North America using Geographic Information Systems (GIS) to quantitatively measure changes in range size and distribution throughout this interval. We specifically considered the role that geographic range size played in mediating extinction resistance and invasion potential of these WIS species. No relationship between geographic range size and survivorship was recovered. However, endemic species with small range sizes were more likely to become invasive. Finally, mollusks did not experience a poleward shift in range out of the tropics during this warm regime. To the extent that these patterns are representative, and the WIS and taxa considered constitute a reasonable ancient analogue to a warmer future world, these results suggest that some biogeographic "rules" may not prevail under Greenhouse conditions of long-term, equable warmth. They also suggest other factors beyond geographic range size,

including distinctive niche characteristics, may play quite important roles in species survival and invasion potential. This potentially complicates predictions regarding the future responses of extant species to long-term warming.

Introduction

Scientists predict significant climatic warming in the near future even under the most conservative modeling scenarios (e.g., Sala et al. 2000; Solomon et al. 2007; Moss et al. 2010; Burrows et al. 2011), and the consequences pose severe risks to the planet's biota. Taxa will be threatened not only by changing climate (e.g., Travis 2003; Colwell et al. 2008; Harley 2011; Willis and MacDonald 2011), but also by the species invasions likely precipitated by this change (Stachowicz et al. 2002; Hickling et al. 2006; Thomas and Ohlemüller 2010; Harley 2011). The fossil record can contribute a significant and unique perspective towards understanding the biotic effects of climate change (e.g., Vermeij 1991a,b; McKinney 1997; Liow 2007; Jablonski 2008; Lockwood 2008; Franks and Beerling 2009; Stigall 2010; Dietl and Flessa 2011; Willis et al. 2010; Willis and MacDonald 2011) because it provides the opportunity to monitor species' responses across the entire lifetime of the species. Paleobiogeographic studies are especially important in this regard because geographic range has long been known to have a significant influence on extinction risk (e.g., Hansen 1980; Jablonski 1987, 2008; Flessa and Jablonski 1996; Gaston 2003; Purvis et al. 2000; Kiessling and Baron-Szabo 2004; Jablonski and Hunt 2006; Liow 2007; Payne and Finnegan 2007; Powell 2007; Kiessling and Aberhan 2007; Hendricks et al. 2008; Crampton et al. 2010; Stigall 2010; Harnik 2011; although see Stanley 1986; Stanley et al. 1988; Norris 1992; Vermeij 1993 for notable exceptions) and invasion potential (e.g., Vermeij 1991b; Mouton and Pimm 1986; Roy et al. 1991; Daehler and Strong 1993; Rode and Lieberman 2004; Hayes and Barry 2008). In this contribution we use Geographic Information Systems

(GIS) to examine the influence of geographic range size on both survivorship and invasion potential during the Late Cretaceous. GIS-based techniques are frequently used to investigate evolutionary patterns and processes as they allow for quantitative analysis of distribution and range size (e.g., Rode and Lieberman 2004; Stigall and Lieberman 2006; Costa et al. 2008; Hendricks et al. 2008; Kozak et al. 2008; Swenson 2008; Stigall 2010; Myers and Lieberman 2011; Dunhill 2012). We focus specifically on bivalve, cephalopod, and gastropod species from the North American Western Interior Seaway (WIS) because these taxa are diverse and abundant and further, because this region and time interval are well characterized both paleobiologically and geologically (e.g., Hancock and Kauffman 1979; Hattin 1982; Barron 1983; Kauffman 1984; Jablonski 1987; Glancy et al. 1993; Kauffman and Caldwell 1993; Schroder-Adams et al. 1996; Sageman et al. 1997; Fatherree et al. 1998; Kennedy et al. 1998; Tsujita and Westermann 1998; Poulsen et al. 2001; Huber et al. 1995, 2002; Harries 2003; Yacobucci 2004, 2008; Jenkyns et al. 2004; Keller et al. 2004; Cobban et al. 2006; Landman et al. 2007, 2012; Ufnar et al. 2008).

The Late Cretaceous is particularly interesting time for paleobiogeographic analysis because it was a “Greenhouse” interval characterized by extreme and equable warmth, with no permanent polar ice and a latitudinal temperature gradient reduced by 50% or more compared to the modern (Barron 1983, 1995; Covey et al. 1996; Huber et al. 2002; Spicer and Corfield 1992; Jenkyns et al. 2004; Hay 2008). While unlikely to be a direct analogue, Late Cretaceous warmth may resemble the sort of long-term climatic regime into which our planet is headed and thus provide important input on the biogeographic effects of crossing climatic and other environmental thresholds (Spicer and Corfield 1992; Barron 1995; Covey et al. 1996; Haywood et al. 2011). Thus, studies of this interval may provide a window into the factors influencing future long-term patterns of invasion and extinction.

The Late Cretaceous WIS was a shallow epicontinental sea (e.g., $\leq 300\text{m}$ depth) formed by the inundation of the North American continent by waters from both the boreal Arctic and southern equatorial Tethys seas. Continental flooding was caused by higher global sea levels (up to 300m above modern) in combination with basin formation due to lithospheric flexure and tectonic loading produced by the Rocky Mountain uplift to the west. During the Early Cretaceous, the northern and southern arms of the WIS were episodically connected, however, during the latest Albian/earliest Cenomanian, eustatic sea level rose connecting the northern and southern arms until the end Maastrichtian (~ 35 Myr period) (Hancock and Kauffman 1979; Hattin 1982; Kauffman 1984; Glancy et al. 1993; Kauffman and Caldwell 1993; Schroder-Adams et al. 1996; Kennedy et al. 1998). Due to narrow connections at both the northern and southern ends of the WIS, conditions were likely dominated by restricted marine environments, often including somewhat brackish surface waters and a dysoxic benthos. More normal marine conditions were short-lived (0.5-1Myr) and occurred in close association with tectonoeustatic transgressive peaks (Albian-Cenomanian boundary, Cenomanian-Turonian boundary, Coniacian-Santonian, middle Campanian) (Kauffman 1984; Tsujita and Westermann 1998; Fisher and Arthur 2002).

Methods

Data Collection

A spatiotemporal database was constructed for 63 species of Late Cretaceous WIS mollusks. This dataset included 27 species from eight genera of bivalves (*Agerostrea*, *Anomia*, *Crassostrea*, *Exogyra*, *Ilymatogyra*, *Ostrea*, *Pseudoperla*, and *Pycnodonte*), 27 species from 10 genera of cephalopods (*Actinocamax*, *Actinosepia*, *Baculites*, *Belemnitella*, *Eubaculites*,

Eutrephoceras, *Pseudobaculites*, *Sciponoceras*, *Trachybaculites*, and *Tusoteuthis*), and nine species from five genera of gastropods (*Anisomyon*, *Drepanochilus*, *Euspira*, *Graphidula*, and *Turritella*) (Appendix 2-1 and 2-2). The taxa in this study were chosen because they are common and abundant in the WIS during the Late Cretaceous and are well characterized taxonomically and paleobiologically. Taxa were excluded if they did not meet geographic or stratigraphic resolution standards: locality information at the county-level or better and stratigraphic resolution at the level of geologic stage; geographic resolution of the majority of occurrences was the 1mi² township, range, and section. Further, all included taxa occurred in at least two geographically unique locations within a single geologic stage or in at least one unique location in two or more stages. We recognize that these standards necessarily exclude rare taxa; however, rare taxa are more susceptible to the biases of sampling and preservation. Lazarus taxa (i.e., those present in multiple, non-consecutive geologic stages) were also excluded in order to prevent biases in survivorship and invasions during stages of non-presence (Flessa and Jablonski 1983, Jablonski 1984). Thus, our database reflects a conservative approach, which is likely robust to these biases. The resulting species database consists of 7511 total occurrences, representing 1124 unique geographic localities.

Species identifications and occurrence data were obtained by examination of museum collections by CEM and RAM, and a survey of the literature. The following institutional museum collections were used: Natural History Museum and Biodiversity Institute, University of Kansas (KUMIP); Peabody Museum of Natural History, Yale University (YPM); American Museum of Natural History (AMNH); Texas Memorial Museum, University of Texas–Austin (TMM); University of Montana Paleontology Center (UMPC); United States Geological Survey, Denver, CO (USGS); Academy of Natural Sciences Philadelphia (ANSP), Smithsonian

Institution National Museum of Natural History (NMNH), University of Michigan Museum of Paleontology (UMMP), Sternberg Museum of Natural History, Fort Hays State University (FHSU); University of Nebraska State Museum (UNSM); and the Black Hills Institute (BHI). Fieldwork to obtain new material was also conducted in Colorado, Minnesota, Missouri, Mississippi, North Dakota, and South Dakota by CEM and RAM.

Range Reconstructions

Geographic locality data for species' occurrences were geo-referenced and imported into ARCGIS v. 9.2 for visual representation and spatial analysis (ESRI 2006). PALEOGIS v. 3.0 (Ross and Scotese 2000; Rothwell Group 2007) was then used to reconstruct the paleogeography of each stage during the Late Cretaceous following the methods of Rode and Lieberman (2004) and Stigall and Lieberman (2006) (Figure 3-1). This step ensures that distribution and range area reconstructions minimize estimation error owing to tectonic contraction and expansion in the North American plate over the course of the Late Cretaceous. A stratigraphic database was generated to correlate all geologic formations/members in the Late Cretaceous WIS where species of interest were known to occur. Correlations were determined by extensive literature survey and use of various stratigraphic databases (e.g., USGS National Geologic Map Database: <http://ngmdb.usgs.gov>; Macrostrat: <http://macrostrat.geology.wisc.edu>). Biostratigraphic indices were also used when available following the Late Cretaceous zonation of Cobban et al. (2006).



Figure 3-1. Present day plate reconstruction (a) and PaleoGIS plate reconstruction for the Santonian stage of the Late Cretaceous (b). Available sedimentary record for the Late Cretaceous is shown in black.

Range areas were then estimated by constructing a convex hull around occurrence points for each species during each geologic stage of the Late Cretaceous using the method of Myers and Lieberman (2011) (Figure 3-2; Appendix 2-1). Following Myers and Lieberman (2011), a 10 km buffer was applied to all occurrence points in order to account for errors in translating modern locality information to deep time latitude and longitude. This method also gives area to range reconstructions for species with two or less occurrences in a given stage, allowing them to be retained in the analysis. Previous studies in the Late Cretaceous Gulf and Atlantic Coastal Plain have estimated geographic range as a linear metric (e.g., along-outcrop maximum linear distance between geographic endpoints or maximum great circle distance between occurrences) for a given species at each time interval or for the duration of the species (e.g., Jablonski 1986, 1987; Jablonski and Roy 2003; Jablonski and Hunt 2006; Harnik 2011). This method can be reasonable given the linear geometry of the Gulf and Atlantic Coastal Plain, where area reconstructions would likely erroneously include intervening land. In the WIS basin the use of range area is more informative and meaningful biologically since a linear metric such as described above would necessarily circumscribe some unknown percentage of the perimeter of the species' true distribution, while our reconstructed range areas directly estimate this parameter. Further, it is worth recognizing that when GIS-based paleobiogeographic studies have used both area- and distance-based metrics, they retrieved congruent results (Hendricks et al. 2008; Stigall 2010). However, environments have been shown to change more dramatically in latitudinal than longitudinal space (see Powell 2007 for discussion on the correlation between latitude and environmental tolerance vs. longitude and dispersal ability). Thus, area calculations may be less discerning of species' environmental tolerances because they include the potentially diluting effect of longitudinal range (Stevens 1989; Powell 2007). Consequently, we also estimated

species ranges using the linear metric of latitudinal extent. This was calculated for each species during each stage of the Late Cretaceous by taking the difference in latitude between the most northerly and most southerly occurrence points and adding one (such that species with ranges contained within a single degree of latitude are given non-zero extent) (Appendix 2-1).

Survivorship

Survivorship in a given geologic stage was defined as the presence of a given species in at least one unique locality in the subsequent stage. Thus, a species designated as a survivor in the Cenomanian stage, was one with at least one occurrence in the following Turonian stage. Consequently, species occurring in the Maastrichtian were informative for defining survivorship in the Campanian, however, there were no survivors identified in the Maastrichtian because the Danian stage was excluded from the present analysis.

Paleogene taxa were excluded from our analysis in part because regional occurrence records of such species are rare and hard to verify; e.g., only one of the species we analyzed could demonstrably be shown to occur in Paleogene strata in North America. Moreover, our emphasis was on testing for the effects of geographic range on survivorship and invasion potential during “normal” intervals of prolonged and equable warmth. Survivorship and invasions of Maastrichtian taxa into the Danian might instead reflect the unique environmental changes associated with the end-Cretaceous mass extinction event.

We tested the hypothesis that large range size conferred resistance to extinction during each stage of the Late Cretaceous by looking for a positive correlation between reconstructed range area and species’ survivorship, as well as latitudinal extent and species’ survivorship in subsequent stages. Statistical significance of these correlations was determined by comparing the range size of survivors vs. non-survivors during each stage using a non-parametric Mann-

Whitney U test.

Several contingency table analyses were also used to consider various factors that might be correlated with survivorship. This type of analysis assesses the dependence of two or more properties (Sokal and Rohlf 1995). In our case, such dependence would indicate additional, confounding variables that may reduce our ability to recognize a significant relationship between geographic range and survivorship. For instance, we tested whether extinction resistance was dependent on area of origin by considering the relationship between survivorship and presence in the biogeographic sub-provinces (BSPs) established by Kauffman (1984) for the Late Cretaceous WIS (Figure 3-2).

In an extensive synthesis of the geologic, climatic, oceanographic, and biologic history of the WIS, Kauffman (1984) defined four BSPs, characterized by 10-25% endemic taxa, within the broader North American province. The WIS was divided into three BSPs, from north to south: Northern Interior sub-province (NISP), Central Interior sub-province (CISP), and the Southern Interior sub-province (SISP); the fourth BSP represented the Gulf and Atlantic Coast sub-province (GASP). These BSPs are analogous to modern definitions of biogeographic units; i.e., the NISP is analogous to a cool temperate biotic zone, the CISP is to a mild temperate biotic zone, the SISP to a warm temperate zone, and the GASP to a mixture of southern, warm temperate and subtropical zones. Kauffman (1984) also defined a broad “ecotone” of mixing between BSPs in the north-central WIS, which he identified as the “endemic center” (EC). The EC contained the majority of fauna endemic to the WIS, including several cephalopod and bivalve clades. We also tested whether being an endemic fauna from the EC provided extinction resistance.

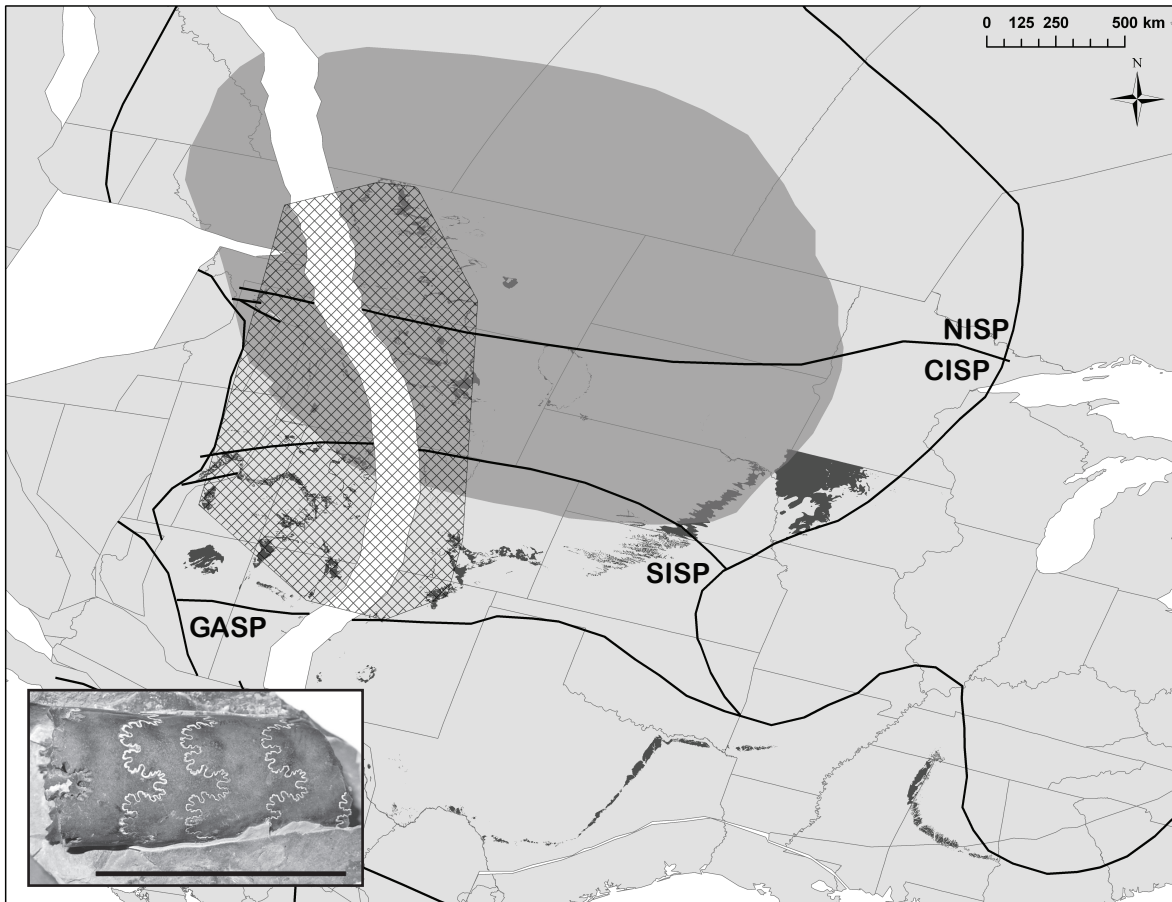


Figure 3-2. Range area reconstruction (hatched) for *Baculites codyensis* (inset) during the Santonian geologic stage. Scale on insert is 2.5cm; available sedimentary record for the Late Cretaceous is shown in black. Estimated shorelines of the WIS as well as BSP delineations are shown in black and Kauffman's Endemic Center in grey. From north-to-south, BSPs are designated: Northern Interior sub-province (NISP), Central Interior sub-province (CISP), Southern Interior sub-province (SISP), Gulf and Atlantic Coast sub-province (GASP). Shorelines, BSPs, and Endemic Center boundaries are modified from Kauffman (1984).

We further tested the relationship between benthic or pelagic adult lifestyles and survivorship during the Late Cretaceous. Gastropods and bivalves were treated as having benthic adults, whereas cephalopods were treated as having pelagic adults. Finally, we tested for differences in survivorship between cephalopods, gastropods, and bivalves.

Invasion Potential

Species invasions were identified when a surviving species expanded its range into a new BSP (*sensu* Kauffman 1984) across a stage boundary. For example, a species was designated as an invader in the Cenomanian stage if that species experienced range expansion from the NISP into the CISP in the Turonian stage (Figure 3-3). The exclusion of Paleogene data from our study again precluded the identification of invasion potential for Maastrichtian species. However, Maastrichtian species did remain informative for the identification of invaders in the Campanian (Appendix). The relationship between range size and invasion potential through time was assessed by comparing ranges (both range area and latitudinal extent) of species that do invade in the subsequent stage with species that do not invade, for all stages using a non-parametric Mann-Whitney U test. The effects of BSP of origin, endemism in the EC, benthic vs. pelagic adult lifestyle, and clade membership on invasion potential were also assessed using contingency table analysis. All statistics were analyzed using PAST v. 2.01 (Hammer et al. 2001).

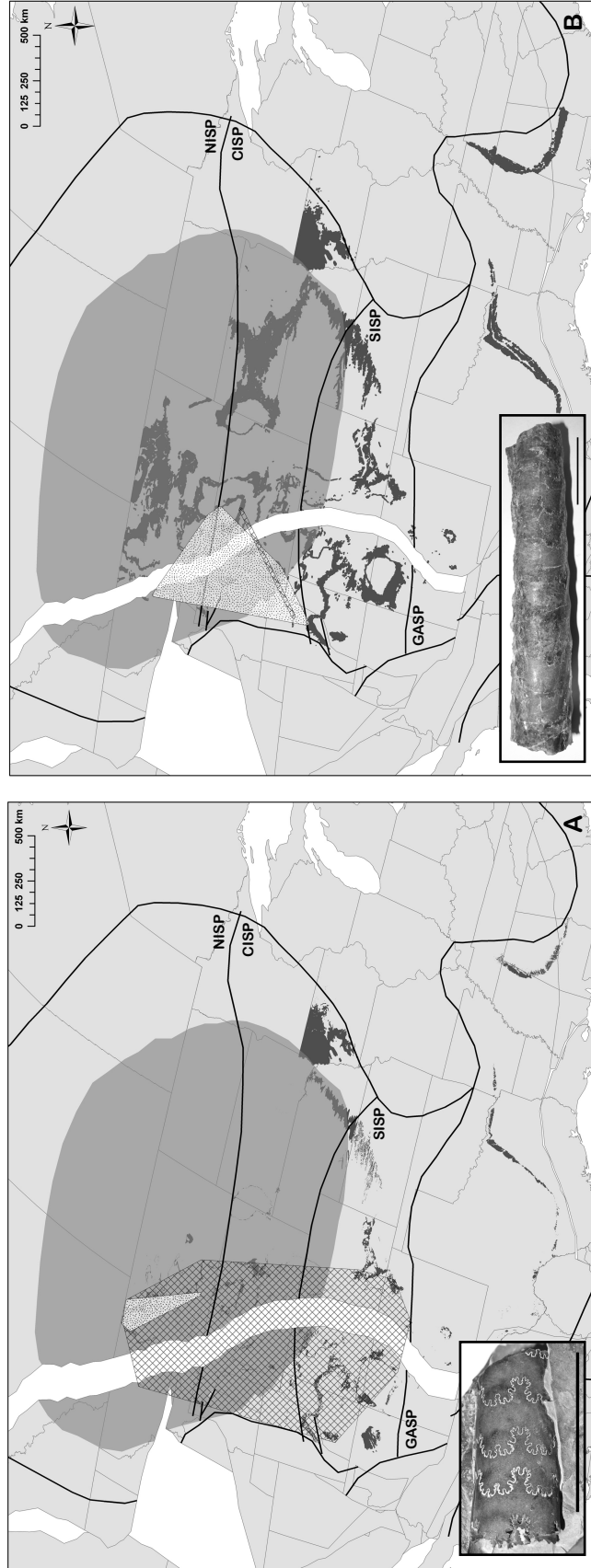


Figure 3-3. Reconstructed ranges for *Baculites codyensis* (hatched, insert panel A) and *B. thomi* (speckled, insert panel B) in the Santonian (A) and Campanian (B) geologic stages. *Baculites codyensis* illustrates non-invasive behavior, i.e., lack of range expansion into new BSPs in the subsequent Campanian stage. *Baculites thomi* does show invasion behavior as characterized by significant range expansion from the Northern Interior BSP in the Santonian into the Central and Southern Interior BSPs in the Campanian. Available sedimentary record for the Late Cretaceous is shown in black. Estimated shorelines of the WIS as well as BSP delineations are shown in black and Kauffman's Endemic Center in grey. Shorelines, BSPs, and Endemic Center boundaries are modified from Kauffman (1984).

Results

Survivorship and Invasion Potential

Molluscan species with larger geographic ranges were not found to be more likely to survive during the Late Cretaceous (Table 3-1). Further, no relationship was recovered between number of BSPs occupied and extinction resistance. Since number of BSPs occupied is related to range size, this corroborates the lack of significant correlation between range area (and latitudinal extent) and survivorship. No significant relationship was resolved between survivorship and BSP of endemism or presence in Kauffman's (1984) EC (Table 3-2); these results are robust to the influence of species' benthic vs. pelagic adult lifestyle as well as to specific clade membership (Table 3-3).

Large range size was also not a significant predictor of invasion potential. Instead, a correlation between small range size and invasion was resolved for taxa across all stages during the Late Cretaceous (range area: $U = 21, p < 0.001$; latitudinal extent: $U = 27, p < 0.001$). When broken into its constituent stages this relationship appears to result from patterns in the Campanian; the Cenomanian and Coniacian stages did not have enough data to be analyzed on their own, and the Turonian and Santonian stages showed a non-significant relationship (Table 3-1). The lack of significance in the Turonian and Santonian may reflect low statistical power of the analyses for these stages resulting from low sample sizes ($n = 2-3$ in Turonian; $n = 3$ in the Santonian). Thus, while a relationship cannot be conclusively documented for all individual stages, generally there does appear to be a negative correlation between range area (and latitudinal extent) and invasion potential when adequate data are available (i.e., during the Campanian and across the whole Late Cretaceous). A significant relationship was also found between invasion potential and number of BSPs occupied, which indicates that endemic species

(i.e., those occupying only a single BSP) were significantly more likely to become invaders than more cosmopolitan taxa (Table 3-2). As with survivorship, no relationship was resolved between invasion potential and BSP of endemism or presence in the EC (Table 3-2). This indicates that Late Cretaceous mollusks were not experiencing a poleward shift in range out of the tropics during this warm regime.

Table 3-1. Mann-Whitney U comparisons of range area and latitudinal extent with survivorship and invasion potential. N designates the number of survivors and non-survivors or invaders and non-invaders respectively for each analysis.

	Range Area Mann-Whitney U	p-value	Latitudinal Extent Mann-Whitney U	p-value
Survivorship				
Late Cretaceous (N = 36, 40)	695	0.799	623	0.314
Cenomanian (N = 4, 6)	9	0.594	10	0.7491
Turonian (N = 5, 8)	19	0.942	10.5	0.093
Coniacian (N = 5, 6)	7	0.167	5	0.080
Santonian (N = 6, 3)	6	0.519	6	0.517
Campanian (N = 16, 17)	107	0.304	114.5	0.448
Invasion Potential				
Late Cretaceous (N = 12, 24)	21	< 0.001	27	< 0.001
Turonian (N = 2, 3)	0	0.149	1	0.387
Santonian (N = 3, 3)	1	0.190	0	0.081
Campanian (N = 6, 10)	3.5	0.004	4	0.005

Table 3-2. Contingency table analysis comparing biotic sub-provinces to survivorship and invasion potential. Endemic species are those that occur in only a single BSP. BSP = biotic sub-province and EC = endemic center of Kauffman 1984.

	Cramer's V	Contingency C	p-value
BSP of occupancy vs. survivorship of endemic species	0.452	0.412	0.081
BSP of occupancy vs. invasion potential of endemic species	0.156	0.154	0.952
No. BSPs occupied vs. survivorship of all species	0.255	0.245	0.167
No. BSPs occupied vs. invasion potential of all species	0.767	0.609	< 0.001
Species endemic to EC vs. survivorship	0.271	0.262	0.120
Species endemic to EC vs. invasion potential	0.026	0.026	0.923

Table 3-3. Contingency table analysis comparing survivorship and invasion potential to benthic vs. pelagic adult lifestyle and clade membership. Endemic species are those that occur in only a single BSP.

	Cramer's V	Contingency C	p-value
Benthic/Pelagic vs. survivorship of endemic species	0.312	0.298	0.073
Benthic/Pelagic vs. survivorship of all species	0.058	0.058	0.606
Benthic/Pelagic vs. invasion potential of endemic species	0.101	0.100	0.707
Benthic/Pelagic vs. invasion potential of all species	0.239	0.233	0.151
Clade vs. survivorship of endemic species	0.325	0.309	0.175
Clade vs. survivorship of all species	0.072	0.072	0.816
Clade vs. invasion potential of endemic species	0.213	0.209	0.727
Clade vs. invasion potential of all species	0.280	0.270	0.243

Assessing External Bias

There are a number of ways in which external biases, reflecting paleobiological incompleteness, may impact our ability to accurately resolve the relationship between biogeographic patterns and survivorship or invasion potential. However, the study area, taxa, and statistical methods used in our analysis were chosen in part to reduce the effects of these biases. As mentioned previously, the Late Cretaceous WIS has a long history of extensive study and paleobiological sampling. Our choice of taxa exclusively included groups with calcitic or aragonitic shelly hard parts and as shown by Kidwell (2005) differences in shell composition do not tend to bias estimations of molluscan species durations in the Phanerozoic (see also Jablonski 1988). Furthermore, the stratigraphic preservation potential in the WIS is generally quite high with no major tectonic activity since the Late Cretaceous to significantly alter deposited sediments. The WIS even contains some exceptional preservation in the form of Konservat Lagerstätte; e.g., the Smoky Hill Chalk, a geographically widespread formation spanning three of the stages included in this study (the Coniacian, Santonian and Campanian stages) (Hattin 1982; Meyer and Milsom 2001; Bottjer 2002). We also used non-parametric statistics, as these are more robust to artifacts arising due to sampling bias (e.g., Jablonski 1987; Jablonski and Valentine 1990; Hunt et al. 2005; Jablonski and Hunt 2006).

Myers and Lieberman (2011) used a variety of tests to assess the quality of the record in this region and specifically the robustness of reconstructed ranges to effects of outcrop availability and sampling. These tests included a resampling procedure to test the effect of far-flung single occurrences on range reconstructions. Similar to the findings of Hunt et al. (2005), these authors found outliers to have little effect on nonparametric rank correlations, and in the WIS it appears that incompleteness had a minimal impact on biogeographic patterns (Myers and

Lieberman 2011). However, to address the potential for sampling bias in the particular dataset used here, we tested for correlation between the number of unique geographic localities in each geologic stage and average reconstructed range area. Were sampling a serious issue, we would expect a significant positive correlation; however, non-parametric Spearman's D and Kendall's τ correlations were not statistically significant at the $p \leq 0.05$ level. We also looked for the effects of outcrop availability on our reconstructed ranges by testing for a correlation between the number of unique geographic localities in each stage and available outcrop area. Again, were available outcrop seriously affecting our reconstructed range sizes, we would expect a significant positive correlation which was not resolved by nonparametric tests (although see discussion in Dunhill 2012 for a different perspective). We further tested for a direct correlation between average reconstructed range size for each stage and available outcrop area; rank correlations remained insignificant (Table 3-4).

Geologic stages in the Late Cretaceous vary in temporal duration (e.g., the Cenomanian stage spans six million years while the Turonian stage spans only four million years). To test for the effect of temporal bin size on range area reconstructions we again looked for a statistically significant nonparametric rank correlation between average range size in a given interval and interval duration. Interval durations were calculated from Cobban et al.'s (2006) zonal table. Were temporal bin size biasing our results we would expect a positive correlation between range size and stage duration, however, neither Spearman's D nor Kendall's τ correlations were found to be significant at the $p \leq 0.05$ level suggesting that bin size was not significantly influencing our results (Table 3-4). A similar result was found by Kennedy and Cobban (1976) who found no relationship between ammonite species longevity, biostratigraphic zone duration, or cycles of transgression and regression.

Table 3-4. Nonparametric rank correlations used to assess issues of external bias in range area analyses. Analyses performed across the six stages of the Late Cretaceous (N = 6 for all tests).

	Spearman's D	p-value	Kendall's τ	p-value
Average No. Unique Occurrences vs. Average Range Area	15.5	0.218	0.414	0.243
Sum of Unique Occurrences vs. Outcrop Area	12	0.142	0.600	0.091
Average Range Area vs. Outcrop Area	40.0	0.749	-0.067	0.851
Average Range Area vs. Interval Duration	40.0	0.749	-0.067	0.851

Discussion

Survivorship and Geographic Range

Contrary to many previous studies (e.g., Hansen 1980; Jablonski 1987, 2008; Flessa and Jablonski 1996; Gaston 2003; Purvis et al. 2000; Kiessling and Baron-Szabo 2004; Jablonski and Hunt 2006; Liow 2007; Payne and Finnegan 2007; Powell 2007; Kiessling and Aberhan 2007; Hendricks et al. 2008; Crampton et al. 2010; Stigall 2010; Harnik 2011), we found no significant relationship between survivorship and range size in 63 species of Late Cretaceous mollusks.

While we acknowledge the low statistical power of some of our range size comparisons (sample sizes provided in Table 3-1), it seems unlikely that this wholly accounts for our results, given that when taxa are binned across the entire Late Cretaceous, a significant relationship between range size and survivorship is still not recovered (Table 3-1). Accordingly, we explore alternative explanations for this pattern.

Many of the studies cited above attribute the positive relationship between survivorship and range size to the buffering effect of large range to local perturbations – i.e., the larger the species' geographic range, the less likely that the species will experience extinction in all of its constituent populations (regardless of the extinction mechanism) (e.g., Kiessling and Aberhan 2007; Foote et al. 2008). Range size can also be viewed as a proxy for the breadth of a species' environmental niche (Stevens 1989; Brown 1995; Brown et al. 1996; McKinney 1997; Stigall 2010), whereby large range size reflects a more generalist, eurytopic species able to survive and proliferate under a greater variety of environmental conditions. The relationship between niche breadth and species longevity has been demonstrated in several studies (e.g., Baumiller 1993; Kammer et al. 1997, 1998; McKinney 1997; Liow 2007; Stigall 2010; Heim and Peters 2011) with the argument that species with greater niche breadth are more resistant to extinction because

they can withstand more significant environmental change within their distribution; stenotopic species with narrower niche breadths are more likely to succumb to extinction given even a small environmental perturbation. In this view, niche breadth is the underlying cause of species survivorship, and range size is correlated with extinction resistance only when positively coupled with niche breadth (i.e., when large range size also reflects large niche breadth) (see Brown 1995 for more on this coupled view).

Notably, the Late Cretaceous is a unique period in Earth history characterized by long-term global warmth, with an important aspect of this warmth being severe reduction in latitudinal temperature gradients (Barron 1983; Spicer and Corfield 1992; Huber et al. 1995, 2002; Hay and DeConto 1999; Jenkyns et al. 2004; Hay 2008). It is reasonable to hypothesize that one biological consequence of this long-term warm and equable climate could be the homogenization of niche breadths amongst species caused by early preferential extinction of more stenotopic species (e.g., Brown 1995; Kammer et al. 1997; Travis 2003; Colwell et al. 2008; Jablonski 2008), and survival of only more eurytopic taxa. This could potentially result in the decoupling of range size from niche breadth, where variability in range sizes no longer necessarily reflects significant changes in niche breadth between species; thus range size would be a poor predictor of extinction resistance. In this scenario, range size would instead be controlled by the complex interaction between species' and organismal traits as suggested by some (e.g., Jablonski 2008; Davidson et al. 2009; Crampton et al. 2010; but see Harnik 2011 for a different perspective).

A number of other factors may be controlling geographic range size in these clades and causing the lack of significant results here. For example, some authors hypothesize that body size (e.g., Johnson et al. 1995; Payne 2005; Liow et al. 2008; Davidson et al. 2009) or abundance (e.g., Stanley 1986; Stanley et al. 1988; McKinney 1997; Payne et al. 2011) are the primary

controls on survivorship, although the direct influence of these has been questioned (e.g., Jablonski 1996, 2008; Kiessling and Baron-Szabo 2004; Harnik 2011). In this scenario, covariation of range size with these factors is the real control on species survivorship, and our results would suggest that range size is perhaps not consistently covarying with these factors during the Late Cretaceous.

Yet another hypothesis, proposed by Waldron (2010), suggests that there may be a difference between “classic” extinction resistance, which can correlate positively with range size, and a species’ “threat tolerance.” Under this premise, if environments change rapidly enough to severely reduce population sizes regardless of niche breadth, such that generalists and specialists have similar range sizes, then generalists lose the advantage of large range size buffering against extinction. At this point, individual species’ tolerances to a given threat will become the significant predictor of survivorship patterns (Waldron 2010). Given the stressors of extreme warmth and fluctuating sea levels, such a scenario is potentially plausible in the Late Cretaceous WIS, and thus the lack of correlation between range size and survivorship in our analysis could reflect the input of individual species’ threat tolerance on survivorship at this time.

Invasion Potential and Geographic Range

In the taxa we analyzed from the Late Cretaceous WIS, small geographic range size was somewhat correlated with an increased potential to invade new areas and there was a significant relationship between endemism and invasion potential (Table 3-2). This may suggest that there is something about being endemic and narrowly distributed in the WIS that ultimately facilitated invasion. However, many other factors may be influencing these results. For instance, by definition a widespread species with a cosmopolitan distribution cannot further invade a “new” region, so this constrains any conclusions somewhat. Moreover, when broken into its constituent

time series, the negative relationship between range size and invasion potential seems to reflect a pull from Campanian taxa, which may imply that conditions after the Campanian were optimal for facilitating invasions. Alternatively, since many taxa originate in the Campanian, the patterns observed here may instead reflect new species that have yet to reach their maximum geographic range, i.e., an *age and area effect* (Gaston 1998; Foote et al. 2008), especially given that only a single species occurs in more than one BSP prior to becoming invasive. It is worth noting that species with small range size, but located near a biogeographic barrier, will in general have a higher probability of invasive behavior due to the fact that even minimal range expansion will likely cause the species to cross into a new biogeographic province. Indeed, Roy (2011) found that localities near the center of biogeographic provinces contained fewer “extralimital species” (i.e., those that have expanded into new provinces) than those near provincial edges. Further, the definition of biogeographic provinces and areas of endemism themselves will play an important role in identifying patterns.

The species considered here also show a complete lack of poleward migration in response to Late Cretaceous warmth. Some studies of extant taxa have predicted such a shift (e.g., Hickling et al. 2006; Parmesan 2006; but see Colwell et al. 2008 and Burrows et al. 2011), whereas here we find no evidence for such a pattern. It is worth noting that Jablonski (2008) has suggested increased global warmth may actually result in a reverse invasion pattern, in which species from higher latitudes migrate into the tropics, filling empty ecological space caused by extinctions in specialized taxa (see also the “ecological opportunity” hypothesis in Vermeij 1991b).

Effects on invasion dynamics, such as those noted here, probably result from a combination of interacting factors (Crawley 1987). As with survivorship, there is ample evidence

that environmental niche breadth may be a significant predictor of invasion potential since greater niche breadth implies greater likelihood to survive in new habitats should they become accessible (see Erhlick 1989; Roy et al. 1991; Brown 1995; Stigall 2010 and references therein). Additionally, body size (Roy et al. 2002), propagule pressure (see Ruiz et al. 2000; Lockwood et al. 2005) and abundance (see Williamson 1996; Williamson and Fitter 1996) may be important components in predicting invasion success. Still, if the results presented here regarding species' invasions during times of extreme warmth are generally representative, they may have some implications for future biotic responses to anticipated long-term warmth; i.e., it may ultimately be the species with initially narrow distributions that become the most effective invaders.

Concluding Remarks

Current work is beginning to investigate the complex relationship between species' abiotic requirements as observed in environmental space (E-space) and how those occur spatially when mapped onto geography (G-space). The relationship between E-space and G-space has strong potential to influence species' distributional limits (e.g., potential for successful dispersal or migration) and the spatial structure of populations (which in turn has a profound effect on patterns of speciation and extinction) (see Soberón and Nakamura 2009; Peterson et al. 2011; Myers & Saupe *in press* for more on these concepts).

Our hope is that the results of this study have provided some interesting patterns relating range size to survivorship and invasion potential during the warm Late Cretaceous interval. A long-standing debate in geology centers on the relative frequency of directional versus cyclical patterns or trends ("Time's Arrow" vs. "Time's Cycle") in the history of the Earth and its life (Gould 1987). Every moment or interval of time is unique, yet because many processes recur, we may study intervals in the distant past to gain understanding of other time periods, even our

own future. The extent to which we can do the latter with the Late Cretaceous WIS is not yet clear. For instance, the WIS was an epicontinental seaway that contained many now extinct clades, and may therefore not serve as a direct analogue to study the effects of future climate changes on marine fauna. Moreover, other sources of human-induced habitat degradation and fragmentation compound the challenges faced by many species today, and will undoubtedly magnify the negative effects of climate change alone (McKinney 1997; Travis 2003; Jablonski 2008; Waldron 2010; Willis and MacDonald 2011).

Still, we suggest that studies of the fossil record in general, and the Late Cretaceous WIS in particular, can provide insight into how species responded biogeographically to long-term “Greenhouse” conditions. The analyses presented here show that some of the biogeographic “rules” prevalent today, and under many other climatic regimes, may not have prevailed under periods of prolonged, extreme warmth. Thus, species may respond to future prolonged warmth in individualistic ways reflecting multifactorial changes in niche and biological dimensions that are species specific (Crawley 1987; Brown et al. 1996; McKinney 1997; Davidson et al. 2009; Waldron 2010; Willis and MacDonald 2011). If broadly applicable, this conclusion may make predictions of future extinctions and invasions even more challenging, as species’ survivorship and invasion potential will not be easily generalizable to a single metric (like geographic range size). An important lesson from the fossil record in this regard is that an approach that applies the tenets of Time’s Cycle in fact validates the importance of Time’s Arrow and the distinctive character of taxon, place, and time.

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Chapter 4. Developing methods for application of ecological niche modeling in the fossil record.

Abstract

Ecological niche modeling (ENM) is a quantitative technique used to predict species' abiotic requirements. It is a correlative technique, requiring geographically explicit information on species occurrences and the suites of environmental conditions experienced at each occurrence point. The output of these models is a set of environmental suitability rules that can be projected geographically and to different time periods to test biogeographic, ecologic, and evolutionary hypotheses. Thus, ENM is a powerful tool for understanding how a dynamic Earth environment impacts biogeographic and macroevolutionary patterns. Although developed by biologists and used extensively in the modern, ENM is just beginning to be applied to the fossil record. In part this reflects the unique methodological challenge of reconstructing paleoenvironmental layers to be used in ENM analysis, whereas in the modern these layers are easily available from large public databases (e.g., WorldClim). This manuscript provides best practices for paleoenvironmental reconstruction to be used in ENM analyses in addition to a discussion of the contextual framework and important considerations to appropriately applying ENM to the fossil record.

Introduction

Ecological niche modeling (ENM) is a widely used technique developed by biologists for estimating species' abiotic environmental requirements (i.e., niche attributes) by correlating known species occurrences with spatially explicit environmental characteristics (Guisan and

Zimmerman 2000; Guisan and Thuiller 2005; Elith and Leathwick 2009; Peterson et al. 2011). This technique allows biologists to quantitatively test hypotheses of species' interactions with their environment across space or into the near future or recent past. Over the last 25 years, ENM has been used to investigate species biogeography (e.g., Svenning and Skov 2004; Graham and Hijmans 2006; Graham et al. 2010), conservation biology (e.g., Martínez-Meyer et al. 2006; Tinoco et al. 2009; Tittensor et al. 2009; Zang et al. 2012), spread of invasive species (e.g., Peterson 2003; Thuiller et al. 2005a; Broennimann et al. 2007; Jiménez-Valverde et al. 2011a) and the effects of predicted climate change (e.g., Pearson and Dawson 2003; Thuiller et al. 2005b; Hijmans and Graham 2006; Saupe et al. 2011). Additionally, when used in conjunction with phylogenetic information, ENM can be used to investigate the conservation or divergence of niche characteristics during evolution. This relationship has also been studied using modern datasets, with increasing support for phylogenetic niche conservatism as the norm in many clades (e.g., Peterson et al. 1999; Graham et al. 2004; Pearman et al. 2008; Weins et al. 2010; Peterson 2011; see Losos 2008 and Losos et al. 2003 for an alternative view).

Whereas modern biologists have extensively used ENM to investigate hypotheses surrounding species' abiotic niches for the last two decades, ENM has only recently been applied to the fossil record (e.g., Stigall Rode & Lieberman 2005a; Stigall and Lieberman 2006; Maguire & Stigall 2009; Svenning et al. 2011). In part, this reflects some methodological challenges in the fossil record not experienced by modern biologists. In the modern, spatially explicit global environmental layers (e.g., temperature, precipitation) are easily downloadable at a variety of spatial scales; however, these layers are not readily available for periods in deep time. Thus, in order to use ENM techniques to quantify niche characteristics, paleontologists must construct their own environmental layers using information from sedimentological and geochemical

analyses. As may be expected, the accuracy and resolution at which paleoenvironments are reconstructed has a significant impact on the quality of the model that is produced. Thus, it is important to have a standardized and quantitative framework for reconstructing past environments to be used in ENM. This manuscript lays out best practices for reconstructing these environmental factors in the fossil record and provides an application of this methodology using data from the Late Cretaceous Western Interior Seaway (WIS) of North America.

ENM: Basic Methods and Theory

Over the last 10 years, ENM has experienced increasing popularity in a number of disciplines and research groups. In part, this reflects the user-friendly nature of many modeling algorithms (e.g., Maxent). However, it is extremely important that ENMs be applied using a reasonable conceptual framework and consideration of species-specific characteristics (Austin 2002, 2007; Guisan and Thuiller 2005; Jiménez-Valverde et al. 2008; Peterson et al. 2011; Araújo and Peterson 2012). Thus, a brief discussion of basic niche modeling theory and methods will provide important context to the way paleoenvironments are reconstructed specifically for ENM in the fossil record. Species geographic distributions are controlled by three main factors: abiotic conditions necessary for species survival and reproduction (e.g., temperature, precipitation), necessary and non-exclusive biotic interactions (e.g., nutrients, mutualisms), and the ability to access suitable areas (e.g., dispersal capacity) (Soberón and Peterson 2005; Peterson et al. 2011). Together, these factors make up the Biotic-Abiotic-Movement, or **BAM**, framework of Peterson et al. (2011; see also Soberón and Peterson 2005; Barve et al. 2011; Saupe et al. 2012). Within this framework, ENM is a multivariate correlative approach for estimating **A**, that is, a species abiotic requirements. In other words, by comparing species' occurrences with the combinations of environmental factors experienced at each location, these

models provide a prediction of what environments are suitable vs. unsuitable for a given species. To the degree that species are able to occupy all suitable abiotic habitat (i.e., are not **B**- or **M**-limited), and that the breadth of habitats reflects the full range of a species environmental tolerances, ENM provides a prediction of a species fundamental niche.

This is different from a mechanistic approach, which identifies species abiotic niche characteristics via direct experimentation or models of the limits of species' physiological tolerances to different environmental factors (Guisan and Zimmerman 2000; Pearson and Dawson 2003; Kearney and Porter 2009). While a mechanistic approach may seem a more robust method for identifying species' environmental requirements, these models also suffer limitations that may lead to inaccuracy in estimating fundamental niche attributes. For example, individual variation in physiological tolerances may lead to an estimate of abiotic limits that does not match those of the entire species – i.e., inaccurate reconstruction of the species-level fundamental niche (see Pearson and Dawson 2003; Kearney and Porter 2009 for more detail on this and other limitations of mechanistic models). Further, the development of physiologically-based models is both expensive and time-consuming – thus, even in the modern, ENM is more widely applied than mechanistic modeling (Barry and Elith 2006; Kearney and Porter 2009).

Significantly, ENMs are able to predict species environmental requirements with high fidelity, even in the fossil record, and therefore are a useful tool for understanding species' interactions with their environment (Pearson and Dawson 2003; Barry and Elith 2006; Elith and Leathwick 2009; Kearney et al. 2010; Walls and Stigall 2012). It is important to note that ENM is not the same as species distribution modeling (SDM), which is a common error in the literature. ENM produces a prediction of species' environmental suitability in *environmental space*. This prediction is often projected onto geography to visualize where suitable vs.

unsuitable environments occur geographically, which outlines *potential* distributions of species. However, in order to estimate actual species' distributions, SDMs must take into account information regarding species' dispersal potential and limitations (Peterson 2006; Peterson et al. 2011; Araújo and Peterson 2012). This may include necessary and/or limiting biotic interactions and barriers to accessing habitable areas, in addition to the abiotic variables used for ENM (for more details see Peterson et al. 2011; Araújo and Peterson 2012; Warren 2012).

Statistical approaches to ENM

Ecological niche modeling may be implemented using a wide variety of modeling algorithms (see Guisan and Zimmerman 2000; Guisan and Thuiller 2005; Elith and Leathwick 2009; Peterson et al. 2011 for a complete overview). The result of most algorithms is a geographically explicit suitability surface that predicts where abiotic conditions are most suitable vs. unsuitable for a given species. This is achieved by fitting one or more statistical functions to explain the relationship between occurrence data and environmental factors (Elith and Leathwick 2009; Peterson et al. 2011). Typically models are trained in a region containing all known species occurrences plus some additional area that is inferred to be accessible, but probably unsuitable, to the species (the **M** region in Soberón and Peterson 2005; Barve et al. 2011; Peterson et al. 2011). Once the algorithm establishes a suitability rule-set for this training region, the model can be projected to a new geographic area and/or to another period of time. The product of this projection is a new geographic map composed of environmental suitability scores for a given species in the new region or time. These results can then be used to test hypotheses of observed distribution changes, extinction, speciation, environmental adaptation, etc.

The primary differences between the available ENM algorithms are the types of species occurrence data required by the model, and the mathematical functions used to generate and test

the model predictions. For example, some models only require information about species presences (e.g., BIOCLIM, DOMAIN), while others require information about both presences and known absences (e.g., generalized additive models – GAMs, generalized linear models – GLMs) (Guisan and Zimmerman 2000; Elith and Leathwick 2009; Peterson et al. 2011). Known absences are challenging to discern in both the modern and fossil records. In the modern, biases in sampling (e.g., not observing a species during a given sampling effort even though it may be present in the area or inability to sample all areas of potential occurrence) prevent most studies from identifying true absences (see Hortal et al. 2008; Jiménez-Valverde et al. 2008, 2011a; Peterson et al. 2011; Martin et al. 2012 for more on this subject). In fossil record, this may reflect imperfect fossil preservation or bias in available geologic outcrop in which fossils may occur. Some modeling algorithms bypass this problem by creating “pseudo-absences” through sampling the environmental background where there are no species’ occurrences (e.g., genetic algorithm for rule-set prediction – GARP), or by sampling from the entire background including species’ occurrences (e.g., a maximum entropy algorithm – Maxent) (Stockwell and Peters 1999; Phillips et al. 2004, 2006; Jiménez-Valverde et al. 2008; Elith and Leathwick 2009; Peterson et al. 2011).

Many research groups have tested the sensitivity, or performance, of the different ENM algorithms under different environmental conditions with mixed results (e.g., Hirzel et al. 2001; Elith et al. 2006; Austin 2007; Elith and Graham 2009; Saupe et al. 2012). However, Maxent and GARP appear to function well under many scenarios, and thus tend to be some of the most widely applied in the modern. Maxent and GARP are also ideally situated to work with fossil data because they deal well with non-uniform and small sample sizes (Peterson 2001; Stigall Rode and Lieberman 2005a; Hernandez et al. 2006; Pearson et al. 2007; see Jiménez-Valverde et al. 2008 and Peterson et al. 2011 for a more complete discussion of how to choose a modeling

algorithm). Whereas Maxent and GARP both use presence-only occurrence data, they differ in the mathematical functions used to predict the relationship between species' occurrences and environmental information (in addition to differences in how they sample for pseudo-absences described above). Maxent estimates suitability via an index of similarity that under most conditions resembles a heterogeneous point process or logistic regression function (Phillips et al. 2004, 2006; Fithian and Hastie 2012; Renner and Warton 2013). Alternatively, GARP uses a machine learning approach that maximizes predictability when a diverse set of locally established suitability rules are tested across an independent set of occurrence and pseudo-absence points (Stockwell and Peters 1999).

Paleoenvironmental Reconstruction

A unique challenge in the application of ENM techniques to test hypotheses in the fossil record is availability of paleoenvironmental information. Spatially explicit environmental layers are easily available in the modern; however, they must be carefully reconstructed in deep time. Environmental layers are constructed by assigning environmental characteristics to unique geographic points from fieldwork and literature survey. GIS algorithms are then used to interpolate between points to create a coverage of values for a particular environmental factor (e.g., temperature) across the area of interest. This procedure is replicated for all environmental factors and time periods of interest (see Stigall Rode and Lieberman 2005a for a detailed description of GIS-based environmental interpolation). Furthermore, traditional environmental information (e.g., temperature, precipitation) are not easily extracted from the geologic record; thus, environmental layers are constructed using sedimentological and geochemical proxies that are considered important in determining habitable areas for marine organisms, as well as reflecting the types of data used by geologists and paleoceanographers to reconstruct marine

paleoenvironments (Boucot 1981; Brenchley and Harper 1998; Stigall Rode and Lieberman 2005a; Walls and Stigall 2011).

When developing paleoenvironmental layers for ENM analysis, there are a number of things to consider in conjunction with aspects of the species' biology under investigation and the types of hypotheses being tested. One is the geographic range of the model that is being built. This has obvious impact on the geographical extent of the paleoenvironmental reconstruction, but also has very important conceptual implications, both on model performance and types of hypotheses that can be tested. A second suite of considerations in preparing for paleoenvironmental analysis is the type of environmental layers (i.e., variables) being reconstructed and how they relate to one another. These concepts are considered in more detail below prior to the discussion of best practices in paleoenvironmental reconstruction.

Determining Model Extent

Several recent studies have noted the importance of delineating an appropriately sized region in which to train niche models (e.g., Guisan and Thuiller 2005; Barve et al. 2011; Peterson et al. 2011; Saupe et al. 2012; Owens et al. *accepted*). ENM algorithms use the training region (**M** in Soberón and Peterson 2005; Barve et al. 2011; Peterson et al. 2011) to sample environments lacking species occurrences in order to determine environmental combinations that are likely unsuitable for a given species. Thus, **M** is the region that could feasibly be sampled (or reached) by a given species and is delimited using information about species' dispersal capabilities. That is, a species that can disperse widely (and thus sample a large number of habitats) should have a larger hypothesized **M** than a species with more limited movement capacity. The size of **M** is important because overestimation will lead models to erroneously predict potentially habitable, but inaccessible areas as unsuitable. Likewise, underestimation of

M will prevent models from having enough information to determine suitability and potentially lead to issues of model extrapolation (Barve et al 2011; Saupe et al. 2012).

Furthermore, it is extremely important when applying ENM that the species occurrence data incorporates the entire species distribution. Application of ENM to specific populations does have interesting applications (see the below section on *ENM in the Fossil Record*).

However, some studies erroneously use population-level occurrence data to build ENMs and then extrapolate these results to the species-level either by directly projecting population models more globally (e.g., Beale et al. 2008; see Araújo et al. 2009 and Jiménez-Valverde et al. 2011b for commentary), or interpreting population-level results at the species' level (e.g., Stigall 2012). This ENM extrapolation has the similar result of limiting the information available to modeling algorithms as they attempt to correlate occurrences with suitable environments (Guisan and Thuiller 2005; Hortal et al. 2008; Jiménez-Valverde et al. 2011b; Raes 2012). The impact on model performance in this case is not entirely clear, but definitely algorithm-dependent. This is because excluded occurrences may truncate species' occupation of environmental space in complex ways that are unique to each situation (Barve et al. 2011; Jiménez-Valverde et al. 2011b; Araújo and Peterson 2012; Raes 2012). Further, due to the differences in how algorithms fit statistical models to occurrence data, the model response to this truncation will be algorithm-dependent (Saupe et al. 2012; Owens et al. *in press*).

Selecting environmental layers for paleo-ENM

Before beginning to collect paleoenvironmental data, it is important to establish what (and how many) environmental layers will be used in the ENM analysis. The types of layers to be used will depend on the scale of the study, the specific ecology of the species under investigation, and the type of data available (Austin 2002, 2007; Guisan and Thuiller 2005; Elith

and Leathwick 2009; Peterson et al. 2011; Araújo and Peterson 2012). For example, in a regional study of benthic marine taxa with presence-only data, abiotic information about substrate conditions, bottom water oxygenation, water depth, wave energy etc. will likely be informative for predicting species environmental requirements. On the other hand, local surface water conditions are unlikely to be as informative both because this variable may not be important at the regional level, and surface conditions may be less significant for benthic taxa (Pearson and Dawson 2003, 2004; Soberón 2007; Peterson et al. 2011 and references therein). The number of layers used is also important: too few layers and ENM algorithms will be challenged to discern environmental differences and prone to over-prediction. Too many layers, however, and the algorithms will produce highly complex, over-fitted models that significantly under-predict suitable environments (Peterson and Cohoon 1999; Barry and Elith 2006; Hernandez et al. 2006; Peterson and Nakazawa 2008; Peterson et al. 2011).

When choosing environmental layers for ENM analysis, direct variables are best. These variables have a direct physiological influence on suitability of habitat for a give species, and in the marine realm, include factors such as temperature, oxygenation, or pH. Indirect variables, on the other hand, do not have direct physiological influence and only affect habitat suitability in that they correlate with one or more direct variables (Austin 2002, 2007; Guisan and Thuiller 2005; Elith and Leathwick 2009; Jiménez-Valverde et al. 2011a; Peterson et al. 2011). Examples of indirect variables in the marine realm include bathymetry or latitude. Unfortunately, in the fossil record, actual measurement of direct variables is impossible. However, what can be measured are proxies for direct variables (e.g., geochemical proxies for temperature, proxies for oxygenation, nutrient availability, light, etc), which would be preferred over proxies for indirect variables for the reasons discussed above.

A final consideration in developing environmental data is correlation between the variables used (e.g., even in the modern, all of the easily downloadable environmental variables are variations of temperature and precipitation). Autocorrelation is common in the modern and fossil records and can lead to issues of overparameterization of model output (i.e., highly complex, over-fitted predictions) among other problems (Guisan and Zimmerman 2000; Elith and Leathwick 2009; Peterson et al. 2011). Thus, it is important to identify and respond to highly correlated environmental variables. A number of solutions to this issue exist, however, the simplest solution is to exclude those variables that are highly auto-correlated (e.g., Guisan and Zimmerman 2000; Guisan and Thuiller 2005; Peterson et al. 2011 and references therein). This can be done easily in R or other statistical package. Another solution is to use principle component analysis (PCA) to distill the contributions of each variable to the overall environmental variance. PCA can also be applied using a simple script in R; after which, the number of components used as environmental layers should reflect some combination of (1) threshold of percent variance explained, (2) a statistical method identifying PC significance (e.g., a broken stick distribution), and (3) a minimum number of layers needed for robust modeling (e.g., 4ish). Elith and Leathwick (2009) and Peterson et al. (2011) provide additional information regarding this and other methods for addressing issues of autocorrelation.

Table 4-1. Coding scheme used in reconstructing the 14 environmental layers for ENM analysis in the Late Cretaceous Western Interior Seaway.

1., 2., 3. Percent clay, silt, sand

Approximate fraction of each grain size within a marine sedimentary package. Modified from Stigall Rode and Lieberman 2005a.

4., 5. Percent carbonate, chalk

Approximate fraction of carbonate (primarily limestone) or specifically chalk beds within a marine sedimentary package. Modified from Stigall Rode and Lieberman 2005a.

6. Substrate Type

Overall character of the substrate on which benthic organisms reside. Decimals delineate relative abundance of substrate types in a sedimentary package. Modified from Stigall Rode and Lieberman 2005a.

1. Sandy: well sorted, coarser-grained sediment
2. Silty: intermediate
3. Muddy: fine-grained, a mixture of silty and soupy sediments
4. Soupy: extremely fine-grained with abundant water in pore spaces

7. Degree of Bioturbation

Approximate degree of burrowing and other within sediment trace fossil activity within a sedimentary package. Decimals delineate relative abundance of trace fossil activity within a sedimentary package.

1. Minimal: less than 25% sediments show bioturbation
2. Moderate: 25-50% sediments show bioturbation
3. Moderate-High: 50-75% of sediments show bioturbation
4. High: 75-100% of sediments show bioturbation

8. Bedding Style

Approximate thickness of sedimentary beds. Decimals delineate relative abundance of bedding thickness in a marine sedimentary package. Modified from Stigall Rode and Lieberman 2005a.

1. Laminated < cm-scale bedding
2. Thin = cm-scale bedding
3. Moderate = dm-scale bedding
4. Thick = m-scale bedding

9. Inferred Water Depth

Relative water depth with respect to storm and fair-weather wave bases. Decimals delineate relative placement within an energy zone. Modified from Stigall Rode and Lieberman 2005a.

0. Subaerial: above mean tide line; including delta plain and marsh settings.

1. Upper Intertidal: between mean low tide and mean high tide; including delta plain and marsh settings.
2. Lower Intertidal: between mean low tide and fair weather wave base; including upper and middle shoreface settings, delta plain and marsh settings.
3. Subtidal: between fair weather and storm wave base; including delta front and prodelta slope settings and lower shoreface settings.
4. Offshore: below storm wave base; including delta front and prodelta slope settings.

10. Depositional Environment

Inferred sedimentary environment of deposition. Decimals delineate relative placement within depositional environments. Modified from Kauffman 1969; Sepkoski 1988; Prothero and Schwab 2004; Neuendorf et al. 2005; Stigall Rode and Lieberman 2005a.

1. Estuarine/Delta Plain: peritidal; beach and channel deposits, high sediment deltaic environments, shallow estuarine
2. Lagoon/Delta Front: near-shore, protected subtidal including shelf lagoons, delta platform, and delta front; frequently heterolithic fine-grained lithofacies with storm deposits; wave-agitated environments including bars, oolite shoals, bioherm-ric areas; above wave base, may or may not be steep
3. Inner Shelf/Prodelta: dominated by sand and silt deposits; shallow open shelf and prodelta environments, below fair-weather wave base, but evidence of storm deposits

4. Midshelf: dominated by dark clay-muds; deeper open shelf and fore-delta environments; fine-grained sediments; low frequency of storm re-working
5. Outer Shelf: dominated by impure clayey carbonate muds; below storm wave base
6. Basin: dominated by carbonate muds; deep water; black shales; lower O₂

11. Oxygenation

Inferred O₂ content of the water column at the water-sediment interface. Decimals delineate relative placement within oxygenation zones. Modified from Sageman and Bina 1997; Brenchley and Harper 1998; Stigall Rode and Lieberman 2005a.

1. Sub-aerial
2. Normal Marine/Aerobic: diverse shelly taxa including epifauna and infauna; bioturbated
3. Dysaerobic: shell epifauna and burrowers dominant; laminated to burrowed sediments
4. Anaerobic: no macrofauna; anaerobic S-bacteria; laminated sediments

12., 13., 14. $\delta^{13}\text{C}$, $\delta^{18}\text{O}$, TOC

Average $\delta^{13}\text{C}$, $\delta^{18}\text{O}$, and total organic carbon per marine sediment package.

Methods for paleoenvironmental reconstruction: an example from the Late Cretaceous

In the Late Cretaceous WIS paleoenvironmental data are being collected for 14 environmental layers (Table 4-1). These include: percent clay, silt, sand, chalk, and carbonate, bedding style, degree of bioturbation, substrate type, inferred water depth, depositional environment, oxygenation, total organic carbon (TOC), $\delta^{13}\text{C}$, and $\delta^{18}\text{O}$. These layers have been modified from those used in previous work (e.g., Stigall Rode and Lieberman 2005a) to reflect the taxa, conditions, and specific hypotheses being tested in the Late Cretaceous WIS. Some modification, however, also reflects evolution of ENM theory and practice. Notably, all environmental layers used are purely abiotic. This is unique from previous work, which incorporated both abiotic and some biotic variables such as ichnofacies or biofacies membership (e.g., Stigall Rode and Lieberman 2005a, Malizia and Stigall 2011; Walls and Stigall 2011; Stigall 2012). The incorporation of biotic variables into the ENM framework is deemed inappropriate here for two reasons: (1) the purpose of ENM in this case is to test hypotheses specific to how species responded to environmental changes, and (2) to the degree that these biotic variables may reflect abiotic conditions, they are indirect proxies and so less desirable (see discussion of direct vs. indirect variables above). While incorporating biotic variables into ENMs may be informative for understanding biotic limitations to species occupation of suitable habitat, they confound the ability to interpret the results that do reflect species' abiotic requirements.

Following previous workers (e.g., Stigall Rode and Lieberman 2005a), paleoenvironmental data is collected primarily through literature survey including peer-reviewed manuscripts, master's theses, doctoral dissertations, and published fieldtrip guidebooks. Additional information gathered from fieldwork should also be incorporated when possible. Standardization of paleoenvironmental coding is extremely important when constructing

environmental layers. This endeavor requires many independent references (e.g., Appendix 3), which use a variety of terminologies, thus consistency in coding is paramount. Table 4-2 shows an example of the coding rule-set used for the Late Cretaceous WIS and associated reference material (Appendix 3).

Substrate conditions are characterized using the environmental layers describing substrate grain size (i.e., percent clay, silt, sand, chalk, and carbonate), substrate type, degree of bioturbation, and bedding style. Percentages are calculated from stratigraphic columns as the approximate fraction of each grain size in a given column. Detailed stratigraphic descriptions in manuscript texts may also be used for this purpose (e.g., Kirkland 1991, Appendix). Figure 4-1 shows a sample stratigraphic column demonstrating the measurement of these properties. In this example, the total vertical extent of each rock type is first calculated by direct measurement: the column is composed of 2.34 m of sandstone, 5.13 m of shale, 1.04 m of siltstone, and 1.64 m of calcareous shale. Using coding rules provided in Table 4-2, sandstone is coded as 100% sand, shale is composed of 50% silt and 50% clay, and siltstone is composed of 87% silt and 17% clay. Likewise, the “calcareous” modifier of the shale is coded as 10% carbonate. Following the calculations shown in Figure 4-1, the lithology of this section is 23.1% sand, 41.0% silt, 34.3% clay, and 1.6% carbonate.

Table 4-2. Late Cretaceous Western Interior Seaway coding rule-set used for evaluating paleoenvironmental information from literature survey.

Sediment Types	Coding	COMMENTS	Citation
siltstone / silt-shale	17% clay, 83% silt	> 66% silt, rest clay	Potter 2005; Prothero & Schwab 2004
claystone / clay-shale	83% clay, 17% silt	> 66% clay, rest silt	Potter 2005; Prothero & Schwab 2004
mudstone / mudrock / shale	50% clay, 50% silt	Potter 2005: mudrock/shale = 50/50 silt/clay Prothero & Schwab 2004: 'mudstone' = 33-65% clay, rest silt (indurated mud)	Potter 2005; Prothero & Schwab 2004
bioclastic mudstone	10% lmst, 45% clay, 45% silt	< 10% lmst, rest mudstone Neuendorf et al. 2005: indurated mud w/ ~ 50/50 clay & silt but not fissile or laminated	Prothero & Schwab 2004; Neuendorf et al. 2005
wackestone	10% lmst, 45% clay, 45% silt	> 10% lmst, rest mudstone Reading 1996: is typical of a lagoonal environ	Prothero & Schwab 2004; Neuendorf et al. 2005
packstone	5% clay, 5% silt, 90% lmst	grain-supported Neuendorf et al. 2005: < 1% mud	Prothero & Schwab 2004
grainstrone	100%	no mud Reading 1996: is typical of a lagoonal to reef flat environ	Prothero & Schwab 2004
marl / marlstone	50% clay, 50% lmst	Pettijohn 1957: 35-65% clay & 65-35% carbonate	Neuendorf et al. 2005; Pettijohn 1957
silicious ooze	15% clay, 15% slt, 10% lmst, 60% SiO ₂	30% nonbiogenic mud(clay & silt), 0-20% calcareous ooze (CaCO ₃ microfossils), & 50-70% SiO ₂ ooze (SiO ₂ microfossils); (based on the "3 component system" of pelagic-hemipelagic sediments)	Reading 1996
calcareous ooze	15% clay, 15% slt, 60% lmst, 10% SiO ₂	30% nonbiogenic mud(clay & slt), 50-70% calcareous ooze (CaCO ₃ microfossils), & 0-20% SiO ₂ ooze (SiO ₂ microfossils); (based on the "3 component system" of pelagic-hemipelagic sediments)	Reading 1996
argillite		any mudrock that has been subjected to low-grade metamorphism	Prothero & Schwab 2004

glauconite		Fe-rich clay; most often found as pellets in sandstones; in agitated, oxidized, normal shallow marine H ₂ O (max 50-200m) pellets may form under locally reduced conditions; large concretions of glauconite only in shallow shelf environments with slow sedimentation rates & starved of siliciclastics	Prothero & Schwab 2004
calcarenite	100% carbonate	> 50% sand-sized grains carbonate	Neuendorf et al. 2005

Inferred Water Depth	Coding	COMMENTS	Citation
shoreface	H ₂ O depth = [1-3]	zone between seaward limit of shore & near-horizontal surface of offshore zone; typically seaward to storm wave base (~10m)	Neuendorf et al. 2005
upper shoreface	lower intertidal [2]	below low tide line; above fair weather wave base	Prothero & Schwab 2004
middle shoreface	lower intertidal [2]	below low tide line; at fair weather wave base	Prothero & Schwab 2004
lower shoreface	subtidal [3]	below low tide line; below fair weather wave base	Prothero & Schwab 2004
delta plain / marsh	sub-aerial to lower intertidal = [0-2]		
delta front	subtidal to offshore = [3-4]		
prodelta	subtidal to offshore = [3-4]		

Depositional Setting	Coding	COMMENTS	Source
estuarine / marginal marine / delta plain	[1]	peritidal; beach/channel deposits, high sedimentation deltaic environs, shallow estuarine	Kauffman 1969; Sepkoski 1988; Prothero &Swab 2004; Neuendorf et al. 2005; Stigall Rode & Lieberman 2005a
lagoons / delta front	[2]	near-shore, protected sub-tidal including shelf lagoons, delta platform, and delta front; frequently heterolithic fine-grained lithofaces with storm deposits; wave-agitated environments including bars, oolite shoals, bioherm-ric areas; above wave base, may or may not be steep	Kauffman 1969; Sepkoski 1988; Prothero &Swab 2004; Neuendorf et al. 2005; Stigall Rode & Lieberman 2005a
inner shelf / prodelta	[3]	dominated by sand & silt deposits; shallow open shelf & prodelta environments, below fair-weather wave base, but evidence storm deposits	Kauffman 1969; Sepkoski 1988; Prothero &Swab 2004; Neuendorf et al. 2005; Stigall Rode & Lieberman 2005a
midshelf	[4]	dominated by dark clay muds; deeper open shelf & fore-delta environments; fine-grained sediments, low frequency of storm re-working	Kauffman 1969; Sepkoski 1988; Prothero &Swab 2004; Neuendorf et al. 2005; Stigall Rode & Lieberman 2005a
outer shelf	[5]	dominated by impure clayey carbonate muds; below storm wave base	Kauffman 1969; Sepkoski 1988; Prothero &Swab 2004; Neuendorf et al. 2005; Stigall Rode & Lieberman 2005a
basin	[6]	dominated by carbonate muds; deep water; black shales; lower O ₂	Kauffman 1969; Sepkoski 1988; Prothero &Swab 2004; Neuendorf et al. 2005; Stigall Rode & Lieberman 2005a

Descriptors	Coding	COMMENTS	Citation
silty	10% silt		Potter 2005
muddy	5% silt, 5% clay	applied to non-mudstones	Potter 2005
clayey	10% clay	> 10% clay	Potter 2005
sandy, pebbly, etc.	10% sand or pebble	> 10% sand or pebble, etc	Potter 2005
calcareous	10% CaCO ₃	> 10% CaCO ₃ ; forams, nannofossil, etc	Potter 2005
silicious	10% SiO ₂	> 10% SiO ₂ ; diatoms, radiolarians, etc	Potter 2005
carbonaceous	1%	> 1% C _{org}	Potter 2005
argillaceous	10% clay	appreciable amount of clay ("argillaceous limestone has significant, but < 50% clay)	Neuendorf et al. 2005
pyritiferous, ferruginous	3%	typically 1-5%	Potter 2005
micaceous, phosphatic, etc	3%	typically 1-5%	Potter 2005
"wkly calc"	0%		
"intermittent"	2%		
"sporadic"	2%		
"thin lenses"	2%		
"very few"	2%		
"abundant"	25%		
"numerous"	25%		
"streaks"	1%		
"grades into..."	25%		
"slightly..."	1%		
"very..."	33%		
"interbedded"	33%		
"some burrowing"	10%		
"poorly"	1%		

The related variable of substrate type, broadly defines conditions of sea floor hardness and nutrient availability (Boucot 1981; Brenchley and Harper 1998). This is calculated by summing the abundance-weighted contributions of sand, silt, clay, and carbonate in a given sedimentary package. In the example provided by Figure 4-1 and using the substrate type coding from Table 4-1, substrate type would be coded as $0.231*[1] + 0.410*[2] + 0.343*[3] + 0.016*[4] = 2.14$. Note that it is highly likely that the variable substrate type is correlated with some (or all) of the grain size variables describing lithology. This is also likely in the case of bioturbation with oxygenation, and depositional environment with inferred water depth. This provides an excellent example of when a PCA or other analysis should be implemented on the environmental variables to either produce new environmental layers composed of principle components, or otherwise reduce or remove the highly correlated variables from the analysis (Guisan and Zimmerman 2000; Guisan and Thuiller 2005; Peterson et al. 2011).

Degree of bioturbation is a measure of the percentage of beds showing signs of burrowing or other trace fossil activity in a sedimentary package. This layer is a multivariate environmental proxy for general habitability of the sea floor, including such factors as oxygenation, current intensity, depth, and sea floor hardness (Brenchley and Harper 1998; Prothero and Schwab 2004). Bedding style is calculated as the abundance-weighted average thickness of the beds in a sedimentary package. Sediments may range from laminated (thickness less than 1cm) to m-scale, which describes the amount of sedimentary input into the marine habitat. Thus, bedding style is a proxy for water depth, turbidity, and energy level of the environment (Prothero and Schwab 2004). Information about bioturbation and bedding style may be estimated directly from stratigraphic columns or otherwise in the lithostratigraphic discussion provided in the accompanying text. In the example provided in Figure 4-1, two units contain

evidence of bioturbation. The sum of these units is 1.14m, which constitutes 11.3% of the section and the coded value for this location. Coding for bedding style is calculated as described for substrate type above.

As discussed in Stigall Rode and Lieberman (2005a), the variable ‘inferred water depth’ is a measure of water depth relative to tides, storm-, and fair-weather wave bases. This is a proxy for light and oxygenation, in addition to water depth and wave energy in a given marine environment (Boucot 1981; Brenchley and Harper 1998). ‘Depositional environment,’ however, measures the inferred environment of sediment deposition and is more a proxy incorporating distance from the shoreline and relative water depth. Characterization of depositional environments is modified from Stigall Rode and Lieberman (2005a) in conjunction with the methods of other authors (Kauffman 1969; Sepkoski 1988; Prothero and Schwab 2004; Neuendorf et al. 2005). Table 4-2 provides an explanation of each inferred depositional environment coded. Measurement of both inferred water depth and depositional environment requires detailed reading of depositional and sedimentological interpretations in literature sources, or direct field observation. These variables are abundance-weighted averages within a given sedimentary package.

For example, Owen et al. (2005) provide the following lithostratigraphic descriptions of members of the Dakota Sandstone in the Chama Basin of New Mexico:

“The Encinal Canyon of the Chama Basin is far enough east to show abundant evidence of deposition in a marginal-marine environment, perhaps in a somewhat protected estuaries, bays, and tidal flats along the western shoreline of the Western Interior seaway during early Cenomanian time. The Oak Canyon was deposited in an offshore marine

environment.... Both Cubero parasequences were deposited as shoreface marine sands, mostly in the middle shoreface zone, but outer shoreface silty sand is more prominent in the lower parasequence. The middle shaley zone was deposited in the adjacent offshore muddy environment.... The Pagate was deposited in a middle and outer shoreface environment that was well populated with burrowing organisms.” (pp. 222-224)

From this information, the depositional environment of the Encinal Canyon Member is estuarine or tidal flats, which based on the coding rules provided in Tables 1 and 2, is coded as 1. The Oak Canyon Member depositional environment is offshore marine. This description is less specific, and so is coded as 3-5 to include the potential contribution of all three offshore shelf marine depositional environments (i.e., inner shelf, mid-shelf, and outer-shelf environments). The Cubero Sandstone Tongue and Pagate Sandstone Tongue represent middle to outer shoreface environments, coded as 3's. The Encinal Member makes up 12% of the section, the Oak Canyon Member makes up 15.5%, the Cubero Sandstone Tongue is 50.7%, and the Pagate Sandstone Tongue is 21.8%. Thus, the depositional environment for this sedimentary package is coded as:

$$1*0.12+3*0.052+4*0.052+5*0.052+3*0.507+3*0.218 = 2.92.$$

The environmental layer ‘oxygenation’ describes the inferred, relative oxygen content at the sediment-water interface (modified from Sageman and Binna 1997; Brenchley and Harper 1998; Stigall Rode and Lieberman 2005a). As with inferred water depth and depositional environment, this variable is also an abundance-weighted average of a sedimentary package based on detailed reading of literature sources or direct field observation. TOC, $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ are all determined directly from laboratory measurements provided in the literature or analysis of samples collected in the field. TOC is an environmental proxy for nutrient availability,

oxygenation, and sedimentation rate, while $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ are proxies for water temperature, salinity, and oxygenation (Boucot 1981; Johnson Ibach 1982; Creaney and Passey 1993; Fürsich 1993; Brenchley and Harper 1998; Tyson 2001; Prothero and Schwab 2004).

ENM in the Fossil Record: case study of the Late Cretaceous WIS

Occurrence data and stratigraphic correlation

Of course before conducting ENM in the fossil record (or the modern), one needs to quantify species distributions. In deep time this requires detailed analyses of taxonomy, localities, and stratigraphy to ensure that the data being entered, which the models ultimately analyze, are accurate (e.g., Myers and Lieberman 2011; Myers et al. 2013). The greater the time spent validating species assignments and distributions, the more confidence one can have that modeled results are accurate. Species occurrence data may be collected through use of museum collections, literature survey, or direct field collection. Importantly, occurrences should be identified to the species level and at a geographic resolution that approximately matches the resolution of paleoenvironmental data (Guisan and Thuiller 2005; Peterson et al. 2011). To this end, a species database has been constructed including over 8500 species occurrence points from the Late Cretaceous WIS. This dataset is composed of 86 species of molluscs, one species of cirriped arthropod, and 10 species of vertebrates (Table 1-1). Species identification and occurrence data were collected in collaboration with Dr. Richard MacKenzie III, by examination of regional and national museum collections, and fieldwork by C.E.M. and Dr. MacKenzie in Colorado, Minnesota, Missouri, Mississippi, North Dakota, and South Dakota. The museum and institutional collections used included: Academy of Natural Sciences, Philadelphia; American Museum of Natural History; Black Hills Institute; Natural History Museum and Biodiversity

Institute, University of Kansas; Peabody Museum of Natural History, Yale University; Smithsonian Institution National Museum of Natural History; Sternberg Museum of Natural History, Fort Hays State University; Texas Memorial Museum, University of Texas—Austin; University of Michigan Museum of Paleontology; University of Montana Paleontology Center; University of Nebraska State Museum; U.S. Geological Survey, Denver. The geographic resolution of this dataset was the county-level or higher; in the majority of cases the resolution of locality information was the one-mile by one-mile Township, Range, and Section BLM grid.

Once collected, species occurrence data must be geo-referenced (i.e., locality information translated into latitude and longitude) and formatted for ArcGIS (ESRI 2006) and ENM algorithm software. Transferring model predictions to different periods in deep time further requires an accurate stratigraphic correlation of fossil-bearing geologic formations across the region of interest. In the Late Cretaceous, a detailed stratigraphic correlation of WIS formations across all of North America has not been done before, and the last geographically large-scale correlation was completed by Cobban and Reeside in 1952. Consequently, an updated stratigraphic database was constructed for the Late Cretaceous WIS (Table 4-3, references in Appendix 3). Stratigraphic correlations were determined by extensive literature survey and the use of various geologic databases (e.g., USGS National Geologic Map Database:

<http://ngmbd.usgs.gov>; Macrostrat: <http://macrostrat.geology.wisc.edu>; and COSUNA,

Correlation of Stratigraphic Units of North America Project). Biostratigraphic indices were also used when available following the Late Cretaceous zonation of Cobban et al. (2006).

Paleoenvironmental data are being collected as described in the previous section. These data reflect point occurrences of paleoenvironmental reconstruction across available Late Cretaceous outcrops in North America (Figure 1-1). The 14 environmental layers will then undergo PCA

and the number of components retained for ENM analysis will incorporate a minimum of four variables and at least 95% of the variance explained.

ENM applications in the fossil record

Once species occurrence data have been collected and stratigraphic correlations and paleoenvironmental layers have been constructed, there are a wealth of hypotheses that can be tested with ENM to better understand the relationship between ecology, evolution, and the environment. Of particular interest (both to modern and paleo-biologists) are the impacts of changing environments on ecological niche stability within species, the influence of niche breadth on extinction and speciation rates among species, and the effect of extinction events on phylogenetic niche conservation. As previously discussed, species abiotic, fundamental niche is defined as the set of physical environmental conditions in which a species may survive (Peterson et al. 2011). Thus, niche stability is characterized by relatively constant fundamental niche dimensions within a species over its duration (Martínez-Meyer et al. 2004; Pearman et al. 2008; Tingley et al. 2009). Niche breadth describes a species' degree of environmental specificity, and niche conservation is the maintenance of similar niche attributes in evolutionarily related species (Wiens and Graham 2005; Wiens et al. 2010; Peterson 2011). Understanding the accuracy and generality of niche stability, breadth, and conservation under periods of environmental change is significant because these properties limit the geographic expansion of species, which mediates allopatric speciation, extinction resistance, patterns of species richness, community structure, and the spread of invasive species (e.g., Kammer et al. 1997; Peterson 2003; Peterson et al. 2005; Wiens and Graham 2005; Araújo and Rahbek 2006; Kozak and Wiens 2006, 2010; Rangel et al. 2007; Tingley et al. 2009; Wiens et al. 2010; Heim and Peters 2011; Stigall 2012; Myers and Saupe 2013).

The Late Cretaceous WIS is an excellent place to apply ENM to test some of these hypotheses, for example across the two different environmental regimes of the Cenomanian-Turonian (C/T, approx. 99.6 – 89.3 Ma) and the Campanian-Maastrichtian (C/M, approx. 83.5 – 65.6 Ma). The Cenomanian and Turonian stages of the Late Cretaceous mark a period of sea level and temperature rise in the WIS, both of which peaked at the C/T boundary. This period was a time of fairly uniform and rapid environmental change where marine environments moved towards open, aerobic conditions. In contrast, during the C/M the WIS experienced a gradual decline in temperature and sea level, including a number of minor sea level fluctuations. Thus during the C/M, species were forced to respond to repeated episodes of sea level change and concomitant changes in water conditions and chemistry (Kauffman 1984; Caldwell and Kauffman eds. 1993; Fisher and Arthur 2002). Additionally, species responded to climate warming across the C/T, as opposed to the cooling associated during the C/M (Spicer and Corfield 1992; Huber et al 1995, 2002; Hay 2008).

Using ENM, niche attributes within and between species throughout the C/T and C/M can be assessed to test hypotheses of the impact of niche characteristics on patterns of speciation and extinction. Regarding niche stability, it will be possible to quantitatively test hypotheses such as, (1) Do surviving species show stability across environmental changes or is survivorship associated with niche expansion? (2) Is niche stability clade-, community-, or ecologically-specific, or universal among species? (3) Do invasive species show niche stability or expansion during invasions? Understanding the dynamics of when/where niche stability occurs informs the degree to which species may adapt to environmental changes occurring locally as well as across their entire distribution and lifetimes (i.e., addresses the question of plasticity in species abiotic requirements and to what degree, and under what environmental conditions) (Martínez-Meyer et

al. 2004; Martínez-Meyer and Peterson 2006; Pearman et al. 2008; Tingley et al. 2009; Walls and Stigall 2011; Monahan and Tingley 2012; Stigall 2012).

Alternatively, niche breadth has been linked with increased species longevity as well as decreased speciation potential. This is hypothesized to be due to the buffering effect of large niche breadth to environmental perturbations and isolation of populations (Eldredge 1989; Baumiller 1993; Kammer et al 1997; Kammer et al. 1998; Liow 2007; Heim and Peters 2011). In this case, ENM can be used to constrain niche dimensions and test hypotheses such as: (1) What is the effect of niche breadth on extinction selectivity across environmental changes? (2) on patterns of distributional change and species invasions? (3) on rates of niche evolution?

In order to test for niche conservation, phylogenetic hypotheses must be reconstructed for target clades. Statistical metrics (Warren et al. 2008, 2010; Broennimann et al. 2012) then measure the degree of similarity between ENM-generated fundamental niche predictions in related species compared to a null model. Using these techniques, it is possible to test a number of hypotheses, including: (1) Are abiotic niches conserved across environmental changes? (2) Is niche conservation (or lack thereof) clade-, community-, ecologically-specific or universal? (3) Does invasion pressure affect whether niches are conserved?

ENM can also be used to test hypotheses at the population-level if full species distributions are not possible to acquire. For example, by modeling different populations within the same species, one could test whether individual populations show niche differentiation (i.e., adaptation) to local environments following climatic or topographic gradients. It would also be possible to track population-level responses to environmental changes using ENM to assess whether specific population characteristics (e.g., geographic breadth, abundance, etc.) influence population distribution, structure, or survivorship.

Conclusions

Ecological niche modeling is an excellent tool for elucidating the relationships among species and their environment. When applied to the fossil record, it has the unique potential to quantitatively test hypotheses regarding the impact of a dynamic planet on species' evolution. A plethora of previous work has shown that evolution is highly dependent on Earth processes (e.g., Raup 1979, 1994; Vrba 1980, 1985; Hallam 1981; Cracraft 1982; Raup and Sepkoski 1982; Knoll 1989; Allmon and Ross 1990; Knoll et al. 1996; Carroll 2000; Lieberman 2000, 2003a,b; Barnosky 2001; Rothschild and Lister 2003; Stigall Rode and Lieberman 2005a,b; Erwin 2006; Lieberman et al. 2007; Maguire and Stigall 2008; Peters 2008). There is broad agreement that large-scale, independent events have significantly impacted evolutionary history by causing major mass extinctions (e.g., Gould 1985, 2002; Erwin 1990; Jablonski and Raup 1995; Jablonski 2001; Alroy 2010; Congreve *in review*). However, an oft-overlooked corollary is how (and to what degree) abiotic variables play in *initiating* evolutionary change (see discussion in Lieberman et al. 2007; Knoll 2012; Myers and Saupe *in press*). The application of ENM techniques has the potential to be a very powerful tool for investigating this issue in addition to other macroevolutionary patterns and processes, such as niche stability and breadth, phylogenetic conservation, and adaptive vs. evolutionary radiations (e.g., Abe and Lieberman 2012; Lieberman 2012).

Notably, ENM in the fossil record requires some additional methodological steps than when applied in the modern. The most important of these steps is that of reconstructing detailed, spatially-explicit paleoenvironments at the highest possible geographic resolution. This manuscript detailed methods for paleoenvironmental reconstruction that can be used as a standard of “best practices” in this procedure and may serve as a guide to future

paleobiogeographers applying this technique to quantitatively test hypotheses of species-environment interactions in the fossil record.

Table 4-3. Stratigraphic correlation of fossil-bearing formations in the Late Cretaceous Western Interior of North America.

Correlations are resolved to the geologic stage level: Berriasian (BERR), Hauterivian (HAUT), Barremian (BARR), Aptian (APT), Albian (ALB), Cenomanian (CEN), Turonian (TUR), Coniacian (CON), Santonian (SAN), Campanian (CAM), and Maastrichtian (MAA), Danian (DAN). Additional abbreviations used: chalk (chk), limestone (lmst), sandstone (ss), shale (sh), group (grp), formation (fm), mbr (member), University of Montana Paleontology Center (UMPC). References provided in Appendix 3.

State	Geologic Unit	Geologic Stage	References and Comments
AL	Arcola Lmst	CAM	COSUNA (CAM)
AL	Bluffport Marl	MAA	COSUNA (MAA); Hancock 1993 (lowMAA Bluffport Mbr/Ripley Fm); Puckett 1997 (MAA Bluffport Mbr/Demopolis Chk)
AL	Eutaw Fm	SAN/CAM	Mancini et al. 1987; Case & Schwimmer 1988; Savrda et al. 1998; Savrda & Nansen 2003; lots other pubs suggest SAN (e.g. King 1990, King et al. 2004, Kiernan 2002, Whetstone & Collins 1982); Kennedy & Cobban 1991 (SAN Tombigbee Sand Mbr of Eutaw Fm); King & Skotnicki 1994 (SAN); Macrostrat (CON-CAM); Mancini & Puckett 2005 (CON/SAN in NE Gulf); Puckett 1997 (SAN); COSUNA (SAN/CAM on Gulf Coast chart, but in a low resolu "TUR-SAN" box on another chart...)
AL	Niobrara Chk	CON-CAM	Shurr et al. 1994 (CON-CAM)
AL	Smoky Hills Chk (Niobrara Chk)	SAN/CAM	Shurr et al. 1994 (SAN/CAM)
AL	Pierre Sh	CAM/MAA	Shurr et al. 1994 (CAM/MAA)
AL	Crow Crk Mbr (Pierre Sh)	CAM	Shurr et al. 1994 (CAM)
AL	De Grey Mbr (Pierre Sh)	CAM	Shurr et al. 1994 (CAM)
AL	Gregory Mbr (Pierre Sh)	CAM	Shurr et al. 1994 (CAM)
AL	Mobridge Mbr (Pierre Sh)	MAA	Shurr et al. 1994 (MAA)

AL	Sharon Springs Sh (Pierre Sh)	CAM	Shurr et al. 1994 (CAM)
AL	Verendrye Mbr (Pierre Sh)	CAM	Shurr et al. 1994 (CAM)
AL	Virgin Mbr (Pierre Sh)	CAM	Shurr et al. 1994 (CAM)
AL	Rotten Lmst	CAM/MAA	Loeblich et al. 1962 (Rotten Lmst = old name for Selma Chk); Harper 1910 (Rotten Lmst = Selma Chk); Salisbury 1895 (Rotten = Selma); White 1887 (Rotten = Austin Chk)
AL	Selma Grp	CAM/MAA	COSUNA (CAM/MAA)
AL	Blufftown Fm (Selma Grp)	CAM	Case & Schwimmer 1988 (in GA), Schwimmer et al. 1993 (mid-CAM in AL/GA), King 1990; Puckett 1992 (CAM); Kennedy & Cobban 1991 (CAM); Becker et al. 2009 (CAM in GA); King & Skotnicki 1994; Becker et al. 2009 (in GA); Macrostrat (SAN/CAM); Puckett 1997 (CAM); COSUNA (CAM)
AL	Demopolis Chk (Selma Grp)	CAM/MAA	Heydari 2001 (CAM/MAA); Kiernan 2002 (CAM/MAA); Mancini et al. 1987 (CAM/MAA); Case & Schwimmer 1988 (CAM/MAA); Puckett 1992 (CAM/MAA); Puckett & Mancini 2000 (MAA); King 1990 (CAM); Mancini et al. 2008 (CAM in Ern Gulf Coast); Locklair & Savrda 1998 (CAM, also in MS,TN); Kennedy & Cobban 2001 (midCAM basal in MS/AL); Becker et al. 2009 (CAM/MAA in MS); King & Skotnicki 1994 (CAM central AL); Macrostrat (CAM/MAA); Mancini & Puckett 2005 (mid/upCAM in NE Gulf); Hancock 1993 (mid/upCAM); Puckett 1997 (CAM/MAA); COSUNA (CAM)
AL	Mooreville Chk (Selma Grp)	CAM	Heydari 2001 (CAM); King et al. 2004 (CAM); Mancini et al. 1987 (CAM); Kiernan 2002 (CAM); Puckett & Mancini 2000 (CAM); Case & Schwimmer 1988 (CAM); Lacklair & Savrda 1998 (CAM); Puckett 1996 (SAN/CAM); Mancini et al. 2008 (SAN/CAM in eastern Gulf Coast); Kennedy & Cobban 1991 (CAM); Becker et al. 2009 (SAN/CAM Mooreville center of state); King & Skotnicki 1994 (CAM); Macrostrat (CAM); Mancini & Puckett 2005 (midSAN/midCAM in NE Gulf); Puckett 1997 (CAM); COSUNA (CAM)
AL	Prairie Bluff Chk (Selma Grp)	MAA	Heydari 2001, King 1990; Mancini et al. 1987; Kiernan 2002; Puckett 1992; Case & Schwimmer 1988; Pitakpaivan & Hazel 1994; Benson & Tatro 1964; Kennedy et al. 2000; Mancini et al. 2008 (MAA in Ern Gulf Coast); Cobban & Kennedy 1995; King & Skotnicki 1994; Stephenson & Reeside 1938 (MAA Prairie Bluff, CAM/MAA Selma Grp; for eastern Gulf Region); Macrostrat (MAA); Hancock 1993 (upMAA); Puckett 1997 (MAA); COSUNA (MAA)
AL	Providence Sand (Selma Grp)	MAA	King 1990; Puckett 1992; King & Skotnicki 1994; Macrostrat (MAA); Puckett 1997 (MAA); COSUNA (MAA)

AL	Ripley Fm (Selma Grp)	MAA	Vermeij & Dudley 1982 (latest CAM-MAA), Heydari 2001 (MAA), King 1990 (CAM/MAA); Pitakpaivan & Hazel 1994 (CAM/MAA) Mancini et al. 1987 (MAA); Kiernan 2002 (MAA); Puckett 1992 (MAA); Puckett & Mancini 2000 (MAA); Case & Schwimmer 1988 (MAA); Benson & Tatro 1964 (CAM/MAA); Mancini et al. 2008 (CAM/MAA in Em Gulf Coast); Lacklair & Savrda 1998 (MAA); King & Skotnicki 1994 (highestCAM/MAA); Stephenson & Reeside 1938 (CAM/MAA Selma Grp; for eastern Gulf Region); Macrostrat (CAM/MAA for whole range GA/AL/MS/AR/TN/MO/MS); Mancini & Puckett 2005 (upCAM/lowMAA in NE Gulf); Hancock 1993 (lowMAA); Puckett 1997 (MAA); COSUNA (MAA)
AL	Cusseta Sand Mbr (Ripley Fm) (Selma Grp)	CAM	King 1990 (CAM); Case & Schwimmer 1988 (CAM); Puckett 1992 (latest CAM/MAA); King & Skotnicki 1994 (latest CAM/MAA Ripley); Stephenson & Reeside 1938 (CAM/MAA Selma Grp; for eastern Gulf Region); Macrostrat (CAM/MAA); Mancini & Puckett 2005 (upCAM/lowMAA Ripley in NE Gulf); Puckett 1997 (CAM/MAA); COSUNA (CAM/MAA)
AL	Tombigbee Sand	CAM	COSUNA (CAM)
AL	Tuscaloosa Grp	CEN-CON	Spangler & Peterson 1950 (APT-CEN in NC); Heydari 2001 (CEN-CON); King 1990 (CEN/TUR); Case & Schwimmer 1988 (CEN); Kennedy & Cobban 1991 (upCEN Tuscaloosa Grp in AL/MS); King & Skotnicki 1994 (CEN); Macrostrat (CEN-SAN); Mancini & Puckett 2005 (midCEN/TUR Tuscaloosa Fm in NE Gulf); COSUNA (CEN-CON)
AL	Coker Fm (Tuscaloosa Grp)	CEN/TUR	Cahoon 1972 (CEN/TUR); Mancini et al. 1987 (CEN/TUR); Coker underlies Gordo; some pubs say just CEN (e.g. King et al. 2004); Kennedy & Cobban 1991 (upCEN Tuscaloosa Grp in AL/MS); King & Skotnicki 1994 (CEN Tuscaloosa); Macrostrat (CEN/TUR); Mancini & Puckett 2005 (midCEN/TUR Tuscaloosa Fm in NE Gulf); COSUNA (CEN/TUR)
AL	Gordo Fm (Tuscaloosa Grp)	CEN/TUR	Cahoon 1972; Gorder overlies Coker; some pubs say just CEN (e.g. King et al. 2004); Mancini et al. 1987 suggest TUR/CON; Kennedy & Cobban 1991 (upCEN Tuscaloosa Grp in AL/MS); King & Skotnicki 1994 (CEN Tuscaloosa); Macrostrat (CEN-CON); Mancini & Puckett 2005 (midCEN/TUR Tuscaloosa Fm in NE Gulf); COSUNA (CEN on one chart, TUR/CON on Gulf Coast chart)
AR	Arkadelphia Marl	MAA (up)	Pitakpaivan & Hazel 1994 (upMAA); Shaw 1967 (upMAA); Becker et al. 2006 (upMAA); Benson & Tatro 1964 (upMAA); Mancini et al. 2008 (in central Gulf Coast, upMAA); Bottjer 1981 (upMAA); Becker et al. 2009 (MAA); Stephenson & Reeside 1938 (upMAA); Macrostrat (MAA)

AR	Brownstown Marl	SAN/CAM	Shaw 1967 (SAN); Baird 1977 (SAN) Becker et al. 2006 (up-mostSAN/lowestCAM); Mancini et al. 2008 (CAM in central/west Gulf Coast); Marks & Stam 1983 (CAM in SW AR); Hazel & Paulson 1964 (CAM); Stephenson & Reeside 1938 (SAN); Macrostrat (SAN/CAM for Brownstown Fm, CAM/MAA for "Brownstown Marl"); Mancini & Puckett 2005 (low/midCAM in NW Gulf); Waggoner 2006 (lowCAM)
AR	Nacatoch Sand	MAA (low)	Pitakpaivan & Hazel 1994 (lowMAA); Shaw 1967 (lowMAA); Becker et al. 2006 (lowMAA); Kennedy et al. 2000 (lowMAA); Benson & Tatro 1964 (CAM/MAA also northern-LA); Mancini et al. 2008 (CAM/MAA in central Gulf Coast and just CAM in western Gulf Coast); Bottjer 1981 (lowMAA); Marks & Stam 1983 (MAA in SW AR); Stephenson & Reeside 1938 (MAA); Macrostrat (MAA); Mancini & Puckett 2005 (upCAM in NW Gulf)
AR	Saratoga Chk	CAM/MAA	Pitakpaivan & Hazel 1994 (CAM); Kennedy & Cobban 1993 (CAM); Summesberger et al. 2007 (CAM); Benson & Tatro 1964 (CAM, also northern-LA); Kennedy et al. 2000 (CAM); Shaw 1967 (CAM/MAA); Bottjer 1985 (MAA); Landry 1984 (MAA); Bottjer 1981 (MAA); Marks & Stam 1983 (MAA in SW AR); Stephenson & Reeside 1938 (MAA); Macrostrat (CAM/MAA); Hancock 1993 (upCAM in TX)
AR	Tokio Fm	CON	Benson & Tatro 1964 (also northern-LA) (CON); Shaw 1967; Mancini et al. 2008 (CON/SAN in central Gulf Coast); Hazel & Paulson 1964 (CON/SAN); Stephenson & Reeside 1938 (CON/SAN); Macrostrat (CON/SAN)
AZ	Dakota Fm	CEN/TUR	Heaton 1950 (CEN); Cobban & Reeside 1952a (CEN); Eaton & Nations 1991 (CEN in Black Hawk Mesa Basin); Kirkland 1991 (CEN in Black Mesa); Leckie et al. 1991 (CEN in Black Mesa); Olesen 1991 (CEN in Black Mesa); Carr 1991 (CEN in Black Mesa); Page & Repenning 1958 (equiv to Graneros in CO = CEN in Black Mesa); Agasie 1969 (CEN); Tibert et al. 2009 (CEN); Macrostrat (APT-TUR "Fm/Grp", BERR-TUR "Grp"); COSUNA (CEN)
AZ	Mancos Fm	CEN/TUR	Heaton 1950 (CEN-CAM); Cobban & Reeside 1952a (CEN/TUR); Eaton & Nations 1991 (CEN/TUR in Black Mesa Basin); Kirkland 1991 (CEN/TUR in Black Mesa); Leckie et al. 1991 (CEN/TUR in Black Mesa); Olesen 1991 (CEN/TUR in Black Mesa); Carr 1991 (CEN/TUR in Black Mesa); Page & Repenning 1958 (equiv to Greenhorn Fm in CO = CEN/TUR in Black Mesa); Shanley & McCabe 1995 (TUR); Bratt 1993 (CEN/TUR at least); Macrostrat (CEN-CAM); COSUNA (TUR)
AZ	Twowells SS (Mancos Sh)	CEN	USGS DB (lower upCEN); Sageman 1996 (upCEN)

AZ	Mesaverde Grp	TUR-SAN	Heaton 1950 (MAA); Young 1957 (lowTUR/upCEN lowest Mesaverde); Cobban & Reeside 1952a (TUR/CON); Eaton & Nations 1991 (TUR-SAN in Black Mesa Basin); Carr 1991 (mid/upSAN Yale Pt SS, upCON/midSAN Wepo Fm, midCON Toreva Fm); Edwards et al. 2005 (Yale Pt SS/Wepo Fm equiv w/ Emery SS in UT = SAN); Shanley & McCabe 1995 (SAN Yale Pt SS, SAN/CON Wepo Fm, TUR/CON Toreva); Irby & Albright 2005 (lowTUR/midCON Toreva Fm); Leckie et al. 1991 (TUR Toreva Fm); Becker et al. 2010 (TUR Toreva Fm); Bratt 1993 (midTUR Toreva SS); Macrostrat (TUR-MAA); COSUNA (CON-MAA Mesaverde Grp, CAM/MAA Yale Pt SS, SAN/CAM Wepo Fm, CON/SAN Toreva Fm); NOTE: Truini & Thomas 2003 and Leidig et al 2005 say Mesaverde Grp = Yale Pt SS, Wepo Fm, & Toreva Fm
AZ	Pinkard Fm	CEN	Cobban & Reeside 1952a (CEN)
CO	Benton Group	CEN/TUR	Schumacher & Everhart 2005 (CEN/TUR for "old Fort Benton Grp" in KS); Bamburak & Nicolas 2009 (ALB/CEN Benton "Fm" or "Sh" in Manitoba); Hattin 1982 (old Benton Fm = Graneros/Grihn/Carlile combined); Cobban & Reeside 1952a (CEN/TUR Benton "Sh"); COSUNA (CEN/TUR)
CO	Burro Canyon Fm	ALB/CEN	Simmons 1957 (correlates w/ Cedar Mtn Fm in UT; Cifelli 1999: Cedar Mtn Fm in UT = ALB/CEN); Aubrey 1989 (ALB); Kirkland et al. 1999 (correlates w/ Cedar Mtn Fm in UT; Cifelli 1999: Cedar Mtn Fm in UT = ALB/CEN); Elder & Kirkland 1993 (ALB); Miller 1987 (correlates w/ Cedar Mtn Fm in UT; Cifelli 1999: Cedar Mtn Fm in UT = ALB/CEN); Macrostrat (HAUT-ALB); COSUNA (BARR-ALB); NONMARINE
CO	Carlile Sh	CEN/TUR	Hattin 1986 (TUR); Elder & Kirkland 1993 (TUR); Heaton 1950 (CEN); Weimer 1960 (at least TUR); Bratt 1993 (midTUR Fairport, Blue Hill, Codell mbrs / Carlile); Tibert et al. 2009 (TUR); Macrostrat (TUR-CON); Cobban & Reeside 1952a (TUR); Lockridge & Scholle 1978 (midTUR); Sageman 1996 (TUR); COSUNA (TUR)
CO	Un-named Mbr (Carlile Sh)	TUR	Hattin 1986 (upTUR); Shurr et al. 1994 (TUR)
CO	Castlegate SS	CAM	Johnson 2003 (CAM); Kirschbaum & Hettlinger 2004 (CAM); USGS DB (lateCAM); Abbott et al. 2007 (CAM); Robinson 2005 (mid/upCAM in UT); Maiall & Arush 2001 (CAM in UT); Robinson & Slingerland 1998 (CAM in UT); Miall 1993 (CAM in UT); Mederos et al. 2005 (CAM); Loseth et al. 2006 (CAM); McLaurin & Steel 2000 (midCAM in UT); York et al. 2011 (mid/upCAM); Aschoff & Steel 2011 (mid/upCAM); Jinnah et al. 2009 (mid/upCAM); Johnson 1987 (CAM); Uroza 2008 (midCAM); Krystinik & DeJarnett 1995 (mid/upCAM)

CO	Colorado Grp	CEN-CAM	see Iowa; Cobban & Reeside 1952a (CEN-CAM); COSUNA (CEN-CON)
CO	Dakota SS	ALB/CEN	Aubrey 1989 (CEN); Hattin 1986 (ALB/CEN); Stephenson & Reeside 1938 (ALB/CEN); Elder & Kirkland 1993 (CEN); Ellis & Tschudy 1964 (CEN); Heaton 1950 (CEN); Johnson 2003 (CEN); Donselaar 1989 (CEN in NM); Lorenz & Cooper 2001 (CEN); Mederos et al. 2005 (CEN); Bratt 1993 (ALB); Tibert et al. 2009 (CEN); Macrostrat (ALB/CEN for Dakota SS in NM, APT-TUR for Dakota Fm/Dakota Grp, BERR-TUR for Dakota Grp); Molenaar 1983 (CEN); COSUNA (APT-TUR Dakota); Cobban & Reeside 1952a (APT-CEN Dakota); Kent 1968 (upALB); Eicher 1965 (CEN top of Dakota); LOWER DAKOTA CAN BE NONMARINE
CO	Fox Hills SS	MAA	Landman & Cobban 2003 (MAA); Carpenter 1979 (MAA); Weimer 1960 (MAA); Haun 1961 (MAA); Cobban & Reeside 1952a (MAA); USGS DB (MAA); Nichols & Fleming 2002 (MAA); Carvajal & Steel 2009 (MAA in WY); Mederos et al. 2005 (MAA); Macrostrat (CAM/MAA); COSUNA (CAM)
CO	Frontier SS	CEN/TUR	Kent 1968 (upTUR); Eicher 1965 (Frontier = Graneros/Greenhorn/lowest Carlile ~ CEN/TUR); Barlow & Haun 1966 (CEN/TUR in WY); Cobban & Reeside 1952b (CEN NONMARINE lower 1/2; TUR/lowestCON marine upper 1/2); Young 1951 (TUR in MT); Johnson 2003 (TUR); Mederos et al. 2005 (CEN/TUR); Macrostrat (TUR for "SS" or ALB-SAN for "Fm"); COSUNA (CEN/TUR)
CO	Fruitland Fm	CAM/MAA	Stephenson & Reeside 1938 (CAM/MAA); Elder & Kirkland 1993 (CAM/MAA); O'Shea 2009 (CAM); Armstrong-Ziegler 1978 (CAM in NM); Cobban 1973 (CAM); Weimer 1960 (CAM); Williamson 1996 (CAM/MAA in NM); Donselaar 1989 (MAA in NM); Palmer & Scott 1984 (MAA in NM); Williamson et al. 2009 (CAM/MAA in NM); Olsen et al. 1999 (CAM at least part); Ambrose & Ayers 2007 (CAM); Lorenz & Cooper 2001 (CAM); Macrostrat (CAM); Cobban & Reeside 1952a (MAA); Molenaar 1983 (CAM/MAA); Jinnah et al. 2009 (upCAM); COSUNA (CAM); NONMARINE
CO	Graneros Sh	CEN/TUR	Aubrey 1989 (CEN); Hattin 1986 (CEN); Phillips et al. 2007 (CEN); Elder & Kirkland 1993 (CEN); Ellis & Tschudy 1964 (CEN); Heaton 1950 (CEN); Weimer 1960 (at least TUR); Lorenz & Cooper 2001 (CEN); Bratt 1993 (CEN); Tibert et al. 2009 (CEN); Macrostrat (CEN); Cobban & Reeside 1952a (CEN); Lockridge & Scholle 1978 (mid/upCEN); Hancock 2004 (low/midCEN); Sageman 1996 (midCEN); COSUNA (CEN)
CO	Thatcher Lmst Mbr (Graneros Sh)	CEN	Lockridge & Scholle 1978 (mid/upCEN); Hattin 1986 (CEN); Bratt 1993 (midCEN); Elder & Kirkland 1993 (CEN)

CO	Greenhorn Lmst	CEN/TUR	Hattin 1986 (CEN/TUR); Phillips et al. 2007 (CEN/TUR); Elder & Kirkland 1993 (CEN/TUR Grnhorn); Heaton 1950 (CEN); Weimer 1960 (at least TUR); Lorenz & Cooper 2001 (CEN/TUR); Bratt 1993 (CEN Lincoln Mbr/Greenhorn); Tibert et al. 2009 (CEN/TUR); Macrostrat (CEN/TUR); Cobban & Reeside 1952a (CEN/TUR); Lockridge & Scholle 1978 (upCEN/midTUR); Molenaar 1983 (TUR); Sageman 1996 (midCEN/midTUR); COSUNA (CEN/TUR)
CO	Bridge Crk Lmst Mbr (Grnhorn Lmst)	CEN/TUR	Lockridge & Scholle 1978 (equiv to Pfeifer, Jetmore, & part-Hartland Sh Mbrs / Greenhorn = latestCEN-midTUR); Hattin 1986 (upmostCEN-TUR); Bratt 1993 (lateCEN-midTUR); Merewether et al. 1975 (CEN/TUR); USGS DB (lateCEN-TUR); Elder & Kirkland 1993 (CEN/TUR); Cadrin et al. 1995 (TUR); Sageman 1996 (upCEN/midTUR)
CO	Hunter Canyon Fm	CAM/MAA	Pranter et al. 2009 (Hunter Canyon Fm = Williams Fork Fm); Payne et al. 2000 (CAM/MAA Williams Fork); Nelson 2003 (CAM Williams Fork); Seidler & Steel 2001 (CAM Williams Fork); Johnson 2003 (CAM/MAA); probably NONMARINE (Williams Fork is dominantly nonmarine)
CO	Iles Fm	CAM	Pranter et al. 2009 (Iles Fm used to be called Mt Garfield Fm); USGS DB (CAM); Johnson & Rice 1990 (CAM/MAA); Payne et al. 2000 (CAM/MAA); Gomez-Veroiza & Steel 2010 (<i>Baculites perplexus</i> to bottom <i>B. cuneatus</i> zones = mid/up CAM); Nelson 2003 (CAM/MAA); Seidler & Steel 2001 (CAM/MAA); Abbott et al. 2007 (CAM/MAA); Diem & Archibald 2005 (CAM/MAA); Loseth et al. 2006 (CAM/MAA); Cobban & Reeside 1952a (CAM); Johnson 1987 (CAM); Uroza 2008 (mid/upCAM); Krystinik & DeJarnett 1995 (mid/upCAM)
CO	Trout Crk SS Mbr (Iles Fm)	CAM	Diem & Archibald 2005 (<i>Exitoloceras jenneyi</i> zone is just below Trout Crk = upCAM, <i>Didymoceras cheyennense</i> zone just above Trout Crk = upCAM); Warner 1964 (Trout Crk equiv to Rollins SS = <i>E. jenneyi</i> zone = upCAM); Finn & Johnson 2005 (CAM); Hettinger & Kirschbaum 2002 (equiv to Rollins SS); Johnson et al. 2005a,b (CAM); Cobban & Reeside 1952a (CAM); Johnson & Rice 1990 (upCAM); Johnson 1987 (CAM); Krystinik & DeJarnett 1995 (upCAM)
CO	Kirtland Sh	CAM/MAA	Stephenson & Reeside 1938 (CAM/MAA); Elder & Kirkland 1993 (MAA); O'Shea 2009 (upmost CAM/MAA); Cobban 1973 (CAM); Weimer 1960 (CAM); Williamson 1996 (CAM/MAA in NM); Williamson et al. 2009 (CAM/MAA in NM); Ambrose & Ayers 2007 (CAM/MAA); Lorenz & Cooper 2001 (MAA); Tibert et al. 2009 (CAM/MAA); Macrostrat (CAM/MAA); Cobban & Reeside 1952a (MAA); Molenaar 1983 (CAM/MAA); Jinnah et al. 2009 (upCAM in part); COSUNA (CAM/MAA); NONMARINE

CO	Laramie Fm	MAA	Carpenter 1979 (MAA); Lockley & Hunt 1995 (MAA); Weimer 1960 (MAA); USGS DB (lateMAA); Nichols & Fleming 2002 (MAA); Cobban & Reeside 1952a (MAA); Eaton & Kirkland 2008 (MAA); Macrostrat (CAM/MAA); COSUNA (CAM/MAA); Landman & Cobban 2003 (MAA); NONMARINE
CO	Lewis Sh	CAM/MAA	Stephenson & Reeside 1938 (MAA); Elder & Kirkland 1993 (CAM); Seidler & Steel 2001 (MAA); O'Shea 2009 (CAM); Cobban 1973 (CAM); Weimer 1960 (CAM); Haun 1961 (CAM/MAA); Williamson 1996 (CAM in NM); Donselaar 1989 (CAM/MAA in NM); Palmer & Scott 1984 (CAM in NM); USGS DB (upCAM/lowMAA); Williamson et al. 2009 (CAM in NM); Olsen et al. 1999 (CAM at least part); Lorenz & Cooper 2001 (CAM); Carvajal & Steel 2009 (MAA in WY); Mederos et al. 2005 (MAA); Tibert et al. 2009 (CAM); Loseth et al. 2006 (MAA); Macrostrat (CON-CAM); Molenaar 1983 (CAM); Jinnah et al. 2009 (midCAM); Uroza 2008 (lowMAA); Krystinik & DeJarnett 1995 (CAM/MAA); COSUNA (CON/SAN)
CO	Mancos Sh	CEN-CAM	Kent 1968 (upALB-SAN in part); Cobban & Reeside 1952a,b (ALB-CAM); Aubrey 1989 (starts upCEN); Eicher 1965 (Mancos = upDakota thru Niobrara ~ CEN-CAM); Stephenson & Reeside 1938 (TUR-CAM); Elder & Kirkland 1993 (CEN-CAM); Heaton 1950 (TUR-SAN); Pranter et al. 2009 (into CAM); Payne et al. 2000 (into CAM); Gomez-Veroiza & Steel 2010 (into upCAM); Cobban 1973 (into CAM); Weimer 1960 (at least TUR-CAM); Johnson 2003 (TUR-CAM); Donselaar 1989 (CEN-CAM in NM); Palmer & Scott 1984 (into CAM in NM); Lorenz & Cooper 2001 (up into CAM); Mederos et al. 2005 (CEN-CAM); Tibert et al. 2009 (CEN-CAM); Macrostrat (CEN-CAM); Molenaar 1983 (CEN-CAM); COSUNA (CEN-MAA)
CO	Buck Tongue (Mancos Sh)	CAM	Johnson 2003 (CAM); Kirschbaum & Hettlinger 2004 (midCAM); USGS DB (midCAM); Hettlinger & Kirschbaum 2002 (CAM); Robinson 2005 (midCAM in UT); Maiall & Arush 2001 (CAM in UT); Robinson & Slingerland 1998 (CAM in UT); Macrostrat (CEN-CAM Mancos); McLaurin & Steel 2000 (midCAM in UT); York et al. 2011 (midCAM); Aschoff & Steel 2011 (midCAM); Johnson 1987 (CAM); Krystinik & DeJarnett 1995 (mid/upCAM); COSUNA (CEN-MAA Mancos)
CO	Corcoran SS Mbr (Mancos Sh)	CAM	Willis & Gabel 2001 (above Sego SS = CAM+); Kirschbaum & Hettlinger 2004 (mid/upCAM); Hettlinger & Kirschbaum 2002 (equiv to Mt Garfield = CAM); USGS DB (CAM); Aschoff & Steel 2011 (upCAM); Macrostrat (SAN/CAM); Nelson 2003 (Corcoran Mbr of Iles Fm, Iles Fm = CAM); Payne et al. 2000 (upCAM); Pranter et al. 2009 (CAM, as mbr of Iles Fm); Warner 1964 (btwn <i>Baculites scotti</i> & <i>Exitoloceras jenneyi</i> zones = mid/upCAM); Johnson 1987 (CAM); Krystinik & DeJarnett 1995 (mid/upCAM); COSUNA (SAN)

CO	Cozzette SS Mbr (Mancos Sh)	CAM	Willis & Gabel 2001 (above Sego SS = CAM+); Kirschbaum & Hettinger 2004 (upCAM); Miall 1993 (above Sego SS, but w/in Price Riv Fm = CAM); Hettinger & Kirschbaum 2002 (equiv to Iles Fm = CAM); USGS DB (CAM); Aschoff & Steel 2011 (upCAM); Macrostrat (CAM); Nelson 2003 (Cozzette Mbr of Iles Fm, Iles Fm = CAM); Payne et al. 2000 (upCAM); Pranter et al. 2009 (CAM, as mbr of Iles Fm); Warner 1964 (top of Cozzette = <i>Exitoloceras jenneyi</i> zone = upCAM); Johnson 2003 (mid/upCAM); Johnson 1987 (CAM); Krystinik & DeJarnett 1995 (mid/upCAM); COSUNA (CAM)
CO	Juana Lopez Mbr (Mancos Sh)	TUR	Hattin 1986 (TUR); Elder & Kirkland 1993 (TUR); Johnson 2003 (TUR); USGS DB (lateTUR); Williamson et al. 2009 (TUR in NM); Tibert et al. 2009 (CEN-CAM Mancos); Edwards et al. 2005 (upTUR in UT); Molenaar 1983 (TUR)
CO	Morapos SS Mbr (Mancos Sh)	CAM	Finn & Johnson 2005 (CAM); Johnson et al. 2005a,b (CAM); Cobban & Reeside 1952a (CAM); Johnson 1987 (CAM); Uroza 2008 (midCAM); Krystinik & DeJarnett 1995 (midCAM)
CO	Mowry Sh Mbr (Mancos Sh)	ALB/CEN	Kent 1968 (upALB); Eicher 1965 (Mowry Sh = top bit Dakota ~ CEN); Phillips et al. 2007 (ALB); Johnson 2003 (CEN); Tibert et al. 2009 (CEN-CAM Mancos); Macrostrat (APT-CEN Mowry Sh/Colorado Grp); Molenaar 1983 (CEN-CAM Mancos); COSUNA (ALB/CEN); Aubrey 1989 (lowCEN Mowry, CEN start of Mancos); Cobban & Reeside 1952b (ALB)
CO	Rollins SS Mbr (Mancos Sh)	CAM	Willis & Gabel 2001 (above Sego SS = CAM+); Kirschbaum & Hettinger 2004 (upCAM); USGS DB (CAM); Aschoff & Steel 2011 (upCAM); Macrostrat (CAM/MAA); Payne et al. 2000 (upCAM); Pranter et al. 2009 (CAM, as mbr of Iles Fm); Warner 1964 (Rollins SS = <i>Exitoloceras jenneyi</i> zone = upCAM); Johnson 2003 (upCAM); Johnson et al. 2005 (equiv to Trout Crk = CAM); Cobban & Reeside 1952a (CAM); Johnson & Rice 1990 (upCAM); Johnson 1987 (CAM); Krystinik & DeJarnett 1995 (upCAM); COSUNA (CAM/MAA)
CO	Menefee Fm	CAM	Cobban & Reeside 1952a (CAM); Weimer 1960 (CAM); Williamson 1996 (CAM in NM); Donselaar 1989 (CAM in NM); Palmer & Scott 1984 (CAM in NM); USGS DB (SAN); Williamson et al. 2009 (SAN/CAM in NM); Olsen et al. 1999 (CAM); Lorenz & Cooper 2001 (CAM); Macrostrat (CON for "Fm, CON/SAN for "Sh Fm"); Molenaar 1983 (CAM); Jinnah et al. 2009 (low/midCAM); MENEFEE IS AT LEAST PARTIALLY NONMARINE

CO	Mesaverde Fm/Grp	CAM/MAA	Stephenson & Reeside 1938 (CAM/MAA); Cobban & Reeside 1952a (CAM/MAA); Heaton 1950 (CAM); Pranter et al. 2009 (CAM/MAA); USGS DB (SAN/CAM); Payne et al. 2000 (CAM/MAA); Nelson 2003 (CAM parts containing Iles and Williams Fork Fm); Seidler & Steel 2001 (CAM/MAA); Weimer 1960 (CAM); Donselaar 1989 (CAM in NM); Palmer & Scott 1984 (SAN/CAM in NM); Olsen et al. 1999 (CAM); Lorenz & Cooper 2001 (CAM); Miall 1993 (CAM/MAA in UT); Mederos et al. 2005 (CAM/MAA); Tibert et al. 2009 (CAM); Macrostrat (TUR-MAA); Molenaar 1983 (CAM); Krystinik & DeJarnett 1995 (CAM/MAA); COSUNA (SAN-MAA); Elder & Kirkland 1993 (CAM); UPPER 1/2 MESASVERDE GRP (WILLIAMS FORK FM) NONMARINE
CO	Mount Garfield	CAM	Pranter et al. 2009 (Iles Fm = Mt Garfield Fm in the Book Cliffs); Cobban 1973 (CAM); Johnson 2003 (CAM/MAA); Kirschbaum & Hettlinger 2004 (upCAM); Cobban & Reeside 1952a (CAM/MAA); Warner 1964 (midCAM); Aschoff & Steel 2011 (midCAM)
CO	Niobrara Fm	CON-CAM	Kauffman et al. 2007 (CON-CAM); Dean & Arthur 1998 (latestTUR-CAM); Hattin 1986 (CON-CAM); Elder & Kirkland 1993 (CON-CAM); Heaton 1950 (CON); Cobban & Reeside 1952a (CON/SAN); USGS DB (upTUR-lowCAM); Tibert et al. 2009 (CON-CAM); Macrostrat (CEN-SAN); Lockridge & Scholle 1978 (lowCON/lowCAM); COSUNA (TUR-SAN)
CO	Pictured Cliffs SS	CAM	Stephenson & Reeside 1938 (MAA); Elder & Kirkland 1993 (CAM); O'Shea 2009 (CAM); Cobban 1973 (CAM); Weimer 1960 (CAM); Williamson 1996 (CAM in NM); Donselaar 1989 (CAM/MAA in NM); Palmer & Scott 1984 (CAM/MAA in NM); Williamson et al. 2009 (CAM in NM); Olsen et al. 1999 (CAM at least part); Ambrose & Ayers 2007 (CAM); Molenaar et al. 2002 (CAM); Lorenz & Cooper 2001 (CAM); Macrostrat (SAN); Molenaar 1983 (CAM); Jinnah et al. 2009 (upCAM); COSUNA (SAN)
CO	Pierre Sh	CAM/MAA	Landman & Cobban 2003 (Douglas to Weld Co = lowestMAA); Dean & Arthur 1998 (CAM to start); Bergstresser & Krebs 1983 (CAM/MAA); Hattin 1986 (CAM low Pierre at least); Elder & Kirkland 1993 (CAM); Heaton 1950 (CAM/MAA); Cobban & Reeside 1952a (CAM/MAA); Weimer 1960 (CAM); USGS DB (CAM/MAA); Tibert et al. 2009 (CAM); Macrostrat (CON-MAA "Fm" or SAN-MAA "Sh Fm"); Lockridge & Scholle 1978 (midCAM/lowMAA); COSUNA (CON-CAM in part)
CO	Beecher Island Sh (Pierre Sh)	MAA	Cobban 1951 (Baculites clinolobatus zone = lowMAA in MT/SD); Griffiths 1949 (equiv to Mobridge Mbr = MAA); Cobban & Reeside 1952a (<i>Baculites baculus</i> to <i>B. grandis</i> zones = lowMAA); Lockridge & Scholle 1978 (upCAM; Beecher Island "zone" in KS/CO named for uppermost Niobrara Fm - the "productive zone" in Niobrara fields)

CO	Loyd SS Mbr (Pierre Sh)	CAM	USGS DB (CAM); Cobban 1962 (<i>Baculites perplexus</i> = midCAM); Uroza 2008 (midCAM); Krystinik & DeJarnett 1995 (midCAM)
CO	Sharon Springs Sh (Pierre Sh)	CAM	Cobban & Reeside 1952a (<i>Baculites gregoryensis</i> to <i>B. asperiformis</i> zones = midCAM); Bertog 2002 (low/midCAM)
CO	Point Lookout SS	CAM	Cobban & Reeside 1952a (CAM); Elder & Kirkland 1993 (CAM); Weimer 1960 (CAM); Williamson 1996 (CAM in NM); Donselaar 1989 (SAN/CAM in NM); Palmer & Scott 1984 (SAN/CAM in NM); Williamson et al. 2009 (CAM in NM); Olsen et al. 1999 (CAM); Lorenz & Cooper 2001 (CAM); Macrostrat (TUR-CEN); Molenaar 1983 (CAM); Jinnah et al. 2009 (upCAM)
CO	Purgatoire Fm	ALB/CEN	Ellis & Tschudy 1964 (ALB); Scott 1970 (ALB); Heaton 1950 (ALB - correlates w/ Kiowa Sh of KS); Macrostrat (BERR-CEN); COSUNA (BERR-CEN)
CO	Sego SS	CAM	Johnson 2003 (CAM/MAA); Kirschbaum & Hettinger 2004 (midCAM); USGS DB (lateCAM); Cobban & Reeside 1952a (CAM); York et al. 2011 (midCAM); Warner 1964 (midCAM); Aschoff & Steel 2011 (midCAM); Johnson 1987 (CAM); Krystinik & DeJarnett 1995 (mip/upCAM); Robinson 2005 (midCAM in UT); Maiall & Arush 2001 (CAM in UT); Robinson & Slingerland 1998 (CAM in UT); McLaurin & Steel 2000 (midCAM in UT)
CO	Trinidad SS	MAA	Cobban & Reeside 1952a (MAA); Elder & Kirkland 1993 (MAA); Meyers & Simoneit 1999 (MAA); Tibert et al. 2009 (CAM/MAA); Macrostrat (SAN/CAM); COSUNA (CAM)
CO	Vermejo Fm	MAA	Cobban & Reeside 1952a (MAA); Elder & Kirkland 1993 (MAA); Weimer 1960 (CAM); Meyers & Simoneit 1999 (MAA); Wolfe & Upchurch 1987 (MAA); Tibert et al. 2009 (MAA); Macrostrat (SAN/CAM); COSUNA (CAM); NONMARINE
CO	Williams Fork Fm	CAM/MAA	Cobban & Reeside 1952a (CAM/MAA); Payne et al. 2000 (CAM/MAA); Nelson 2003 (CAM); Seidler & Steel 2001 (CAM); Abbott et al. 2007 (CAM/MAA); Diem & Archibald 2005 (MAA); Loseth et al. 2006 (CAM/MAA); Uroza 2008 (upCAM/lowMAA); Krystinik & DeJarnett 1995 (CAM/MAA); DOMINANTLY NONMARINE
CO	Lion Canyon SS Mbr (Williams Fork Fm)	MAA	Elder & Kirkland 1993 (upper lowMAA); Cobban & Reeside 1952a (MAA); Johnson 1987 (MAA); Haun 1961 (MAA); Daly 1997 (equiv to Fox Hills SS = MAA); Krystinik & DeJarnett 1995 (lowMAA)
IA	Carlile Sh	TUR	COSUNA (TUR)
IA	Blue Hill Sh (Carlile Sh)	TUR	Shurr et al. 1994 (TUR); Sethi & Leithold 1997 (midTUR in CO)
IA	Codell SS	TUR	Shurr et al. 1994 (TUR)

	(Carlile Sh)			
IA	Fairport Chk (Carlile Sh)	TUR		Shurr et al. 1994 (TUR); Sethi & Leithold 1997 (midTUR in CO)
IA	Colorado Grp	CEN-CAM		Schemel 1950 (equiv to Greenhorn/Graneros = CEN/TUR in other states); Logan 1899 (CEN-CAM Colorado Fm - equiv to Lincoln Lmst Mbr/Niobrara Chk in KS); Iowa Geological Survey says "upper Colorado Grp" = Niobrara Chk & Fort Benton, "lower Colorado Grp" = Graneros/Greenhorn/Carlile --> overall = CEN-CAM; USGS DB (CEN/TUR); Macrostrat (HAUT-SAN Colorado Grp)
IA	Dakota Fm/Grp	ALB/CEN		Schemel 1950 (CEN); Stephenson & Reeside 1938 (CEN in Great Plains); USGS DB (ALB/CEN); Macrostrat (APT-TUR for "Dakota Fm/Dakota Grp", BERR-TUR for "Dakota Grp"); Shurr et al. 1994 (ALB/CEN); COSUNA (ALB/CEN)
IA	Graneros Fm	CEN		Shurr et al. 1994 (CEN); COSUNA (CEN)
IA	Greenhorn Fm	CEN/TUR		Shurr et al. 1994 (CEN/TUR); COSUNA (CEN/TUR)
IA	Niobrara Chk	CON-CAM		Shurr et al. (CON-CAM)
IA	Smoky Hills Chk (Niobrara Chk)	SAN/CAM		Shurr et al. (SAN/CAM)
IA	Ft Hays Lmst (Niobrara Chk)	CON		Shurr et al. (CON)
IA	Pierre Sh	CAM/MAA		Shurr et al. 1994 (CAM/MAA)
IA	Mobridge Mbr (Pierre Sh)	MAA		Shurr et al. 1994 (MAA)
IA	Virgin Mbr (Pierre Sh)	CAM		Shurr et al. 1994 (CAM)
IA	Verendrye Mbr (Pierre Sh)	CAM		Shurr et al. 1994 (CAM)
IA	De Grey Mbr (Pierre Sh)	CAM		Shurr et al. 1994 (CAM)
IA	Crow Crk Mbr (Pierre Sh)	CAM		Shurr et al. 1994 (CAM)
IA	Gregory Mbr (Pierre Sh)	CAM		Shurr et al. 1994 (CAM)
IA	Sharon Springs Sh	CAM		Shurr et al. 1994 (CAM)

	(Pierre Sh)		
KS	Carlile Sh	TUR	Hattin 1995 (TUR); Hattin 1986 (TUR); Everhart 2005 (TUR); Cobban & Reeside 1952a (TUR); Shurr et al. 1994 (TUR); Stephenson & Reeside 1938 (TUR in Great Plains); Macrostrat (TUR-CON); Schumacher & Everhart 2005 (TUR); Hattin & Siemers 1987 (TUR); Lockridge & Scholle 1978 (midTUR); Cobban et al. 1959 (TUR); Sageman 1996 (TUR); COSUNA (TUR)
KS	Blue Hill Sh (Carlile Sh)	TUR (mid)	Bratt 1993 (midTUR); Hattin 1995 (mid TUR); Hattin 1986 (TUR); Schumacher & Everhart 2005 (midTUR); Hattin & Siemers 1987 (TUR); Shurr et al. 1994 (TUR); Cobban & Reeside 1952a (TUR); Lockridge & Scholle 1978 (midTUR); Sethi & Leithold 1997 (midTUR in part in CO); Cobban et al. 1959 (TUR)
KS	Codell SS (Carlile Sh)	TUR (mid)	Bratt 1993 (midTUR); Hattin 1995 (mid TUR); Hattin 1986 (TUR); Macrostrat (TUR); Schumacher & Everhart 2005 (upTUR); Hattin & Siemers 1987 (TUR); Shurr et al. 1994 (TUR); Cobban & Reeside 1952a (TUR); Lockridge & Scholle 1978 (midTUR); Cobban et al. 1959 (TUR)
KS	Fairport Chk (Carlile Sh)	TUR (mid)	Bratt 1993 (midTUR); Hattin 1995 (mid TUR); Hattin 1986 (TUR); Schumacher & Everhart 2005 (midTUR); Hattin & Siemers 1987 (TUR); Shurr et al. 1994 (TUR); Cobban & Reeside 1952a (TUR); Lockridge & Scholle 1978 (midTUR); Sethi & Leithold 1997 (midTUR in CO); Cobban et al. 1959 (TUR)
KS	Juana Lopez Mbr (Carlile Sh)	TUR	Hattin 1986 (TUR); Elder & Kirkland 1993 (TUR); Johnson 2003 (TUR); USGS DB (lateTUR); Williamson et al. 2009 (TUR in NM); Tibert et al. 2009 (CEN-CAM Mancos); Edwards et al. 2005 (upTUR in UT); Juana Lopez is a mbr of Mancos Sh in CO
KS	Dakota Fm	ALB/CEN	Hattin 1995 (ALB/CEN); Shurr et al. 1994 (ALB/CEN); Cobban & Reeside 1952a (CEN); Sageman 1996 (midCEN); COSUNA (CEN)
KS	Graneros Sh	CEN/TUR	Hattin 1995 (midCEN); Hattin 1986 (CEN); Brenner et al. 2000 (CEN); Liggett et al. 2005 (CEN); Cobban & Reeside 1952a (midCEN); Shurr et al. 1994 (CEN); Hamilton 1994 (CEN); Stephenson & Reeside 1938 (CEN/TUR in Great Plains); Macrostrat (CEN); Schumacher & Everhart 2005 (midCEN); Hattin & Siemers 1987 (CEN); Lockridge & Scholle 1978 (mid/upCEN); Cobban et al. 1959 (CEN); Sageman 1996 (CEN); COSUNA (CEN)
KS	Greenhorn Lmst	CEN/TUR	Hattin 1995 (CEN/TUR); Hattin 1986 (CEN/TUR); Brenner et al. 2000 (CEN/TUR); Liggett et al. 2005 (CEN Lincoln Lmst Mbr); Schumacher 2008 (TUR upGreenhorn); Cobban & Reeside 1952a (midCEN/lowTUR); Shurr et al. 1994 (CEN/TUR); Stephenson & Reeside 1938 (TUR in Great Plains); Macrostrat (CEN/TUR); Schumacher & Everhart 2005 (CEN/lowTUR); Hattin & Siemers 1987 (CEN/TUR); Lockridge & Scholle 1978 (upCEN/midTUR); Cobban et al. 1959 (CEN/TUR); Sageman 1996 (CEN/TUR); COSUNA

			(CEN/TUR)
KS	Hartland Sh (Greenhorn Lmst)	CEN (up)/TUR (low)	Hattin 1995 (upCEN/lowTUR); Hattin 1986 (CEN/TUR); Schumacher & Everhart 2005 (upCEN); Hattin & Siemers 1987 (CEN/TUR); Cobban & Reeside 1952a (CEN); Lockridge & Scholle 1978 (upCEN/lowTUR); Cobban et al. 1959 (upCEN); Sageman 1996 (upCEN/lowTUR)
KS	Jetmore Sh (Greenhorn Lmst)	TUR (low)	Hattin 1995 (lowTUR); Hattin 1986 (TUR); Schumacher & Everhart 2005 (upCEN/lowTUR); Hattin & Siemers 1987 (TUR); Bottjer 1978 (lowTUR); Cobban & Reeside 1952a (TUR); Lockridge & Scholle 1978 (lowTUR); Bottjer et al. 1978 (lowTUR); Sageman 1996 (lowTUR)
KS	Lincoln Lmst (Greenhorn Lmst)	CEN (up)	Hattin 1995 (upCEN); Hattin 1986 (CEN); Schumacher & Everhart 2005 (mid/upCEN); Hattin & Siemers 1987 (CEN); Cobban & Reeside 1952a (CEN); Lockridge & Scholle 1978 (upCEN); Liggett et al. 2005 (CEN); Cobban et al. 1959 (CEN); Sageman 1996 (upCEN)
KS	Pfeifer Sh (Greenhorn Lmst)	TUR (low/mid)	Hattin 1995 (low/midTUR); Hattin 1986 (TUR); Schumacher & Everhart 2005 (lowTUR); Hattin & Siemers 1987 (TUR); Cobban & Reeside 1952a (TUR); Lockridge & Scholle 1978 (low/midTUR); Sageman 1996 (low/midTUR)
KS	Niobrara Chk	CON-CAM	Hattin 1995 (CON-CAM); Everhart 2005 (CON-CAM); Everhart 2001 (CON-CAM); Hattin 1982 (CON-CAM Smokey Hill Chk/NIO); Carpenter et al. 1995 (CON-CAM); Cobban & Reeside 1952a (CON-SAN); Shurr et al. 1994 (CON-CAM); Stephenson & Reeside 1938 (CON/SAN in Great Plains); Macrostrat (CEN-SAN); Hattin & Siemers 1987 (TUR-CAM); Shurr et al. (CON-CAM in MT/MN/IA); Bertog 2010 (ends lowCAM); Lockridge & Scholle 1978 (CON/lowCAM); Cobban et al. 1959 (CON/SAN in part); COSUNA (TUR-SAN in part)
KS	Ft Hays Lmst (Niobrara Chk)	CON	Hattin & Siemers 1987 (CON), Hattin 1995 (CON); Shurr et al. 1994 (CON in MT/MN/IA); Hattin 1986 (CON); Everhart 2001 (CON); Cobban & Reeside 1952a (CON); Cobban et al. 1959 (CON); COSUNA (CON)
KS	Smoky Hills Chk (Niobrara Chk)	CON-CAM	Hattin 1995 (CON-CAM); Macrostrat (SAN "Chk", CON/SAN "Mbr"); Hattin & Siemers 1987 (CON-CAM); Shurr et al. 1994 (SAN-CAM in MT/AL/SD/MN/IA); Hattin 1986 (SAN/CAM); Everhart 2001 (CON-CAM); Cobban & Reeside 1952a (CON/SAN); Cobban et al. 1959 (CON/SAN in part); COSUNA (SAN in part)

KS	Pierre Sh	CAM/MAA	Shurr et al. 1994 (CAM/MAA in MT/AL/SD/MN/IA), Hattin & Siemers 1987 (CAM lower part); Hattin 1986 (CAM to start); Bertog 2010 (CAM to start); Cobban & Reeside 1952a (CAM/MAA); Lockridge & Scholle 1978 (midCAM/lowMAA); Koch 1967 (Pierre in western KS/eastern CO = Judith Riv/Claggett Fm in MT = CAM/MAA); COSUNA (CON-CAM in part)
KS	Beecher Island Sh (Pierre Sh)	MAA	Cobban 1951 (lowMAA - <i>Baculites clinolobatus</i> zone in MT/SD); Griffiths 1949 (equiv to Mobridge Mbr = MAA); Cobban & Reeside 1952a (lowMAA - equiv to Mobridge, <i>B. baculus/B. grandis</i> zones); Lockridge & Scholle 1978 (upCAM; Beecher Island "zone" in KS/CO named for uppermost Nio Fm - the "productive zone" in Nio fields)
KS	Gammon Ferruginous Mbr (Pierre Sh)	CAM (low)	Bertog 2010 (lowCAM); Bertog 2002 (lowCAM)
KS	Lake Creek Sh (Pierre Sh)	CAM (up)	Cobban & Reeside 1952a (<i>Baculites compressus</i> zone = upCAM); Hattin & Siemers 1987 (<i>B. reesidei</i> zone = upCAM); Landman et al. 2010 (<i>B. reesidei</i> zone = upCAM); Griffiths 1949 (Lake Creek overlies Weskan, underlies Salt Grass in CO = CAM); Koch 1967 (Lake Crk in wes KS/east CO = Judith River Fm in MT = CAM/MAA)
KS	Salt Grass Sh (Pierre Sh)	CAM (up)	Cobban & Reeside 1952a (<i>Baculites compressus</i> zone = upCAM); Hattin & Siemers 1987 (<i>B. eliasi</i> zone = upCAM)
KS	Sharon Springs Sh (Pierre Sh)	CAM (mid)	Hattin & Siemers 1987 (<i>Baculites obtusus</i> zone = midCAM); Shurr et al. 1994 (CAM in MT/AL/SD/MN/IA); Hattin 1986 (CAM); Bertog et al. 2007 (low/midCAM in Black Hills); Bertog 2010 (midCAM); Cobban & Reeside 1952a (<i>Baculites gregoryensis</i> to <i>B. asperiformis</i> zones = midCAM); Koch 1967 (Weskan in western KS/eastern CO = Claggett Fm in MT = CAM)
KS	Weskan Sh (Pierre Sh)	CAM	Hattin & Siemers 1987 (CAM); Bertog et al. 2007 (midCAM in Black Hills); Bertog 2010 (midCAM); Bertog 2002 (midCAM); Cobban & Reeside 1952a (<i>Baculites gregoryensis</i> zone = midCAM); Landman et al. 2010 (<i>B. compressus/B. cuneatus</i> zones = upCAM); Koch 1967 (Sharon Spgs in west KS/east CO = Judith River Fm in MT = CAM/MAA)
LA	Annona Chalk	CAM	COSUNA (CAM)
LA	Arkadelphia	MAA	COSUNA (MAA)
LA	Austin Group	CON-CAM	COSUNA (CON-CAM, same for Austin Chk)
LA	Brownstown Fm	CAM/MAA	COSUNA (CAM/MAA)
LA	Eagle Ford Grp	CEN/TUR	COSUNA (CEN/TUR)
LA	Fredericksburg Grp	ALB	COSUNA (ALB)

LA	Benbrook Mbr (Goodland Lmst) (Fredericksburg Grp)	ALB	COSUNA (ALB)
LA	Goodland Lmst (Fredericksburg Grp)	ALB	COSUNA (ALB)
LA	Mary's Creek (Fredericksburg Grp)	ALB	COSUNA (ALB)
LA	Marlbrook Marl	CAM	COSUNA (CAM)
LA	Nacatoch Fm	MAA	COSUNA (MAA)
LA	Navarro Grp	MAA	COSUNA (MAA same for Navarro Fm)
LA	Ozan Fm	CAM	COSUNA (CAM)
LA	Paluxy Fm	ALB	COSUNA (ALB)
LA	Pepper Sh	CEN	COSUNA (CEN)
LA	Rapides Fm	CON/SAN	COSUNA (CON/SAN)
LA	Saratoga Fm	CAM/MAA	COSUNA (CAM/MAA)
LA	Selma Grp	SAN-MAA	COSUNA (SAN-MAA)
LA	Selma Chk Selma Grp	CAM/MAA	COSUNA (CAM/MAA)
LA	Taylor Grp	CAM/MAA	COSUNA (CAM/MAA)
LA	Tokio Fm	SAN	COSUNA (SAN)
LA	Tuscaloosa Grp	CEN/TUR	COSUNA (CEN/TUR)
LA	lower Tuscaloosa Fm (Tuscaloosa Grp)	CEN	COSUNA (equiv to Woodbine Fm = CEN)
LA	middle Tuscaloosa Fm (Tuscaloosa Grp)	CEN/TUR	COSUNA (CEN/TUR)
LA	Harris Sand (Tuscaloosa Grp)	CEN/TUR	COSUNA (CEN/TUR)
LA	upper Tuscaloosa Fm (Tuscaloosa Grp)	TUR	COSUNA (TUR)
LA	Washita Grp	ALB/CEN	COSUNA (ALB/CEN)
LA	Buda Lmst (Washita Grp)	CEN	COSUNA (CEN)

LA	Denton Sh (Washita Grp)	ALB	COSUNA (ALB)
LA	Duck Creek Fm (Washita Grp)	ALB	COSUNA (ALB)
LA	Fort Worth Lmst (Washita Grp)	ALB	COSUNA (ALB)
LA	Grayson Marl (Washita Grp)	CEN	COSUNA (CEN)
LA	Kiamichi Fm (Washita Grp)	ALB	COSUNA (ALB)
LA	Main Street Lmst (Washita Grp)	CEN	COSUNA (CEN)
LA	Pawpaw-Weno Fm's (Washita Grp)	ALB	COSUNA (ALB)
LA	South Tyler Fm (Washita Grp)	CEN	COSUNA (CEN)
MO	McNairy Sand	MAA	Gallagher et al. 2005; fieldwork - Crowley's Ridge & Purina kitty litter mine
MO	Owl Crk Fm	MAA	Gallagher et al. 2005; fieldwork - Crowley's Ridge & Purina kitty litter mine
MS	Coffee Sand	CAM	Case & Schwimmer 1988 (CAM); Harrison & Litwin 1997 (CAM in TN); Kennedy & Cobban 1991 (CAM); Macrostrat (SAN/CAM)
MS	Eutaw Fm	SAN/CAM	Kaye & Russel 1973 (SAN); Heydari 2000, 2001 (SAN/CAM); Puckett 1992 (SAN/CAM); Case & Schwimmer 1988 (SAN/CAM, mainly SAN); Macrostrat (CON-CAM); Mancini & Puckett 2005 (CON/SAN in NE Gulf); Hazel & Paulson 1964 (CON/SAN lower Eutaw); COSUNA (SAN/CAM)
MS	Mooreville Chk	CAM	Heydari 2000, 2001 (CAM); Puckett 1992 (CAM); Puckett & Mancini 2000 (CAM); Kennedy & Cobban 1991 (CAM); Becker et al. 2009 (SAN/CAM central AR); Macrostrat (CAM); Mancini & Puckett 2005 (midSAN/midCAM in NE Gulf); Hazel & Paulson 1964 (CAM)
MS	Prairie Bluff Chk (Owl Creek Fm)	MAA	Heydari 2000, 2001 (MAA); Puckett 1992 (MAA); Case & Schwimmer 1988 (MAA Owl Crk); Cobban & Kennedy 1995 (MAA); Stephenson & Reeside 1938 (MAA Prairie Bluff in eastern Gulf Region); Macrostrat (MAA); Mancini & Puckett 2005 (MAA); Hancock 1993 (upMAA)

MS	Ripley Fm	MAA	Vermeij & Dudley 1982 (CAM/MAA); Heydari 2000, 2001 (MAA); Puckett 1992 (MAA); Puckett & Mancini 2000 (MAA); Case & Schwimmer 1988 (MAA); Mancini et al. 2008 (CAM/MAA in eastern Gulf Coast); Macrostrat (CAM/MAA); Mancini & Puckett 2005 (upCAM/lowMAA in NE Gulf); Hancock 1993 (lowMAA)
MS	McNairy Sand Mbr (Ripley Fm)	MAA	Harrison & Litwin 1997 (MAA); Heydari 2000, 2001 (MAA); Case & Schwimmer 1988 (MAA); Macrostrat (MAA); Mancini & Puckett 2005 (upCAM/lowMAA Ripley in NE Gulf)
MS	Rotten Lmst	CAM/MAA	Loeblich et al. 1962 (Rotten Lmst = old name for Selma Chk); Harper 1910 (Rotten Lmst = Selma Chk); Salisbury 1895 (Rotten = Selma Chk); White 1887 (Rotten = Austin Chk)
MS	Selma Chalk	CAM/MAA	Macrostrat (CAM/MAA); COSUNA (CAM/MAA for Selma Grp); NOTE: if same as Selma Grp in AL & TN, then definitely CAM/MAA
MS	Tupelo Marl	CAM	Case 1991 (upCAM - Tupelo "Tongue" of Coffee Sand Fm); Monroe 1947 (CAM, Tupelo "Tongue" of Coffee Sand overlies Mooreville Chk in AL/MS); Stephenson & Monroe 1938 (Tupelo "Tongue" overlies Coffee Sand = CAM); Mancini et al. 1995 (CAM, Tupelo "Tongue" underlies Dermopolis chk & overlies Coffee Sand); Macrostrat (CAM for Tupelo Mbr/Coffee Sand); Liu 2007 (CAM Tupelo "Tongue"); Heydari 2000 (Tupelo "Tongue" = lowest mbr Dermopolis Chk = Tibbee Crk Mbr = CAM); Mancini et al. 2008 (midCAM Tupelo "Tongue"); Mancini & Puckett 2005 (midCAM "Tongue"); Hazel & Paulson 1964 (CAM)
MS	Tuscaloosa Fm	CEN-CON	Heydari 2000, 2001 (CEN-CON); Case & Schwimmer 1988 (CEN); Kennedy & Cobban 1991 (upCEN Tuscaloosa Grp in AL/MS); Macrostrat (CEN-SAN); Mancini & Puckett 2005 (midCEN/TUR Tuscaloosa Fm in NE Gulf); COSUNA (CEN-CON Tuscaloosa Grp, upper Tuscaloosa = TUR/CON, "marine Tuscaloosa" = CEN, lower Tuscaloosa = CEN)
MT	Belle Fourche Fm	CEN	UMPC strat chart (CEN/TUR); Condon 2000 (midCEN); USGS DB (CEN); Farquharson & Grotho 1981 (CEN); Rice & Cobban 1977 (CEN); Macrostrat (ALB/CEN "Fm", CEN "Sh"); Cobban & Larson 1997 (low/midCEN); Yang 2011 (mid/upCEN in southern Alberta); Yang & Miall 2010 (mid/upCEN in southern Alberta); Oboh-Ikuenobe et al. 2007 (CEN); Rice 1984 (CEN); COSUNA (CEN)
MT	Mosby SS Mbr (Belle Fourche Fm)	CEN	Condon 2000 (late-midCEN); Oboh-Ikuenobe et al. 2007 (CEN); Rice 1984 (CEN)

MT	Bearpaw Sh	CAM/MAA	Heaton 1950 (MAA); Stephenson & Reeside 1938 (MAA); Nichols & Sweet 1993 (CAM/MAA); Tibert et al. 2009 (CAM/MAA in northern Plains); Roberts et al. 2005 (upCAM); Swift et al. 1985 (MAA in central Rockies); USGS DB (upCAM/lowMAA); Hicks et al. 1995 (CAM/MAA in WY); Condon 2000 (upCAM/lowMAA); Wilson 2006 (CAM/MAA); Finn 2010 (MAA); Rice & Cobban 1977; Bibler 1985 (CAM/MAA); Macrostrat (CAM/MAA); UMPC strat chart (CAM); Farquharson & Grobbo 1981 (CAM/lowMAA); McMannis 1965 (upper Montanan = upper 1/3 LateCret); Fuentes et al. 2011 (CAM); Rice 1980 (CAM); Scherzer & Varricchio 2010 (CAM/MAA); Hancock 1993 (upCAM); Jinnah et al. 2009 (upCAM at least in part); Krystinik & DeJarnett 1995 (upCAM/lowMAA); COSUNA (CAM/MAA)
MT	Carlile Sh	TUR	Shurr et al. 1994 (TUR); UMPC strat chart (TUR/CON); Farquharson & Grobbo 1981 (TUR/CON); Cobban & Larson 1997 (mid/upTUR); Yang 2011 (TUR/CON in southern Alberta); Nielsen 2008 (TUR/lowCON); COSUNA (TUR/CON)
MT	Blue Hill Sh (Carlile Sh)	TUR	Shurr et al. 1994 (TUR); UMPC strat chart (TUR/CON Carlile); Sethi & Leithold 1997 (midTUR in part in CO)
MT	Codell SS (Carlile Sh)	TUR	Shurr et al. 1994 (TUR); UMPC strat chart (TUR/CON Carlile)
MT	Fairport Chk (Carlile Sh)	TUR	Shurr et al. 1994 (TUR); UMPC strat chart (TUR/CON Carlile); Sethi & Leithold 1997 (midTUR in CO)
MT	Un-named Mbr (Carlile Sh)	TUR	Hattin 1986 (upTUR); Shurr et al. 1994 (TUR); UMPC strat chart (TUR/CON Carlile)
MT	Cody Sh	CON-CAM	Heaton 1950 (midSAN in WY); Nichols & Sweet 1993 (CEN-SAN); Tibert et al. 2009 (CON in northern Plains); USGS DB (CEN-CAM); Finn 2010 (CON-CAM); Macrostrat (CEN-SAN); Farquharson & Grobbo 1981 (CON/SAN); COSUNA (CON-CAM)
MT	Claggett Fm	CAM	Heaton 1950 (CAM); Stephenson & Reeside 1938 (CAM); Nichols & Sweet 1993 (CAM); Tibert et al. 2009 (CAM in northern Plains); Roberts et al. 2005 (CAM); Swift et al. 1985 (CAM in central Rockies); Shelton 1965 (CAM start); Hicks et al. 1995 (CAM in WY); Payenberg et al. 2002 (CAM); Payenberg et al. 2003 (CAM); He et al. 2005 (CAM); Condon 2000 (midCAM); Roger & Brady 2010 (CAM); Finn 2010 (CAM); Rice & Cobban 1977 (CAM); Macrostrat (CAM); Bertog et al. 2007 (midCAM); Bertog 2002 (midCAM); UMPC strat chart (CAM); Farquharson & Grobbo 1981 (CAM); McMannis 1965 (mid-Montanan = upper 1/3 LateCret); Payenberg et al. 2002 (CAM); Scherzer & Varricchio 2010 (CAM); Hancock 1993 (low/midCAM); Jinnah et al. 2009 (low/midCAM); Krystinik & DeJarnett 1995 (midCAM); COSUNA

			(CAM)	
MT	Coberly Gulch Fm (Colorado Grp)	CEN/TUR	USGS DB (early Late Cret ~ CEN/TUR); Macrostrat (CEN/TUR); Wallace et al. 1990 (~91-89Ma, up-mostCEN-midTUR); Farquharson & Grotbo 1981 (TUR); McMannis 1965 (lowest LateCret ~ CEN/TUR); Wallace et al. 1990 (upCEN/midTUR); COSUNA (CEN-SAN CO Grp, CEN/TUR Coberly Fm)	
MT	Eagle SS	SAN/CAM	Heaton 1950 (SAN/CAM); Stephenson & Reeside 1938 (SAN/CAM); Nichols & Sweet 1993 (CAM); Roberts et al. 2005 (into CAM); Asquith 1970 (CAM in WY); Shelton 1965 (CAM); Hicks et al. 1995 (CAM in WY); Payenberg et al. 2002 (SAN/CAM); Payenberg et al. 2003 (SAN/CAM); Robinson et al. 1959 (CAM); He et al. 2005 (CAM); Condon 2000 (upSAN/lowCAM); Roger & Brady 2010 (CAM); Foreman et al. 2008 (CAM); Finn 2010 (CAM); Rice & Cobban 1977 (SAN/CAM); Macrostrat (TUR-CAM); Bertog et al. 2007 (top = lowCAM); Bertog 2002 (top = lowCAM); UMPC strat chart (CAM); Farquharson & Grotbo 1981 (upSAN/lowCAM); McMannis 1965 (low Montanan = mid-LateCret); Nielsen 2008 (CAM); Rice 1980 (lowCAM); Jinnah et al. 2009 (lowCAM); Krystinik & DeJarnett 1995 (lowCAM); COSUNA (CAM)	
MT	Fox Hills SS	MAA	Heaton 1950 (MAA in WY); Stephenson & Reeside 1938 (MAA in Great Plains); Nichols & Sweet 1993 (MAA); Tibert et al. 2009 (MAA in northern Plains); USGS DB (MAA); Asquith 1970 (MAA in WY); Hicks et al. 1995 (MAA in WY); Condon 2000 (lowMAA); Russell 1930 (MAA); Wilson 2006 (MAA); Rice & Cobban 1977 (MAA); Macrostrat (CAM/MAA); UMPC strat chart (CAM); Cobban & Larson 1997 (upCAM/lowMAA); Rice 1980 (upmostCAM/MAA); Hancock 1993 (lowMAA); Krystinik & DeJarnett 1995 (MAA); COSUNA (MAA)	
MT	Frontier Fm	CEN/TUR	Farquharson & Grotbo 1981 (CEN/TUR); Dyman et al. 1996 (CEN/TUR); Young 1951 (TUR); USGS DB (ALB-CON); Macrostrat (ALB-SAN)	
MT	Dakota Fm	ALB/CEN	Shurr et al. 1994 (ALB/CEN); COSUNA (ALB)	
MT	Graneros Sh	CEN	Shurr et al. 1994 (CEN); UMPC strat chart (ALB/CEN); Farquharson & Grotbo 1981 (ALB/CEN)	

MT	Greenhorn Fm	CEN/TUR	Heaton 1950 (TUR in WY); Stephenson & Reeside 1938 (TUR in Great Plains); Tibert et al. 2009 (CEN/TUR in northern Plains); Swift et al. 1985 (CEN/TUR in central Rockies); USGS DB (CEN/TUR); Condon 2000 (CEN/TUR); Rice & Cobban 1977 (CEN/TUR); Macrostrat (CEN/TUR); Shurr et al. 1994 (CEN/TUR); UMPC strat chart (TUR); Farquharson & Grotbo 1981 (TUR); Young 1951 (TUR); Cobban & Larson 1997 (upCEN/lowTUR); Nielsen 2008 (TUR); Rice 1984 (CEN/TUR)
MT	Hell Creek Fm	MAA	COSUNA (MAA)
MT	Horsethief SS	CAM/MAA	Heaton 1950 (CAM/MAA); Roberts et al. 2005; USGS DB (lateCAM/earlyMAA); Roger & Brady 2010 (CAM/MAA); Carpenter & Alf 1994 (CAM); Thomas 1978 (CAM/MAA); Rice & Cobban 1977 (MAA); Bibler 1985 (CAM/MAA); Macrostrat (CAM/MAA); Farquharson & Grotbo 1981 (CAM); Fuentes et al. 2011 (CAM); Mudge & Sheppard 1968 (CAM); Rice 1980 (CAM/lowestMAA); Krystinik & DeJarnett 1995 (upCAM); COSUNA (CAM/MAA); COSUNA (CEN/TUR)
MT	Judith River Fm (= Parkman Fm)	CAM/MAA	Heaton 1950; Stephenson & Reeside 1938; Nichols & Sweet 1993 (CAM); Tibert et al. 2009 (CAM in northern Plains); Roberts et al. 2005 (CAM); Rice & Shurr 1980 (CAM/MAA); Hicks et al. 1995 (CAM in WY); Becker et al. 2009 (CAM/MAA); Condon 2000 (lateCAM); Roger & Brady 2010 (CAM); Rogers et al. 2010 (CAM); Foreman et al. 2008 (CAM); Koenig et al. 2009 (CAM); Finn 2010 (CAM/MAA); Macrostrat (CAM); Bertog et al. 2007 (midCAM lower part); Bertog 2002 (midCAM at least); UMPC strat chart (CAM); Farquharson & Grotbo 1981 (CAM); McMannis 1965 (middle Montanan = upper 1/3 LateCret); Nielsen 2008 (CAM); Rice 1980 (mid/upCAM); Scherzer & Varricchio 2010 (CAM); Hancock 1993 (Parkman = midCAM); Jinnah et al. 2009 (midCAM in WY, mid/upCAM in MT); Krystinik & DeJarnett 1995 (upCAM); COSUNA (CAM); predominantly NONMARINE
MT	Lennepe SS	CAM/MAA	Stephenson & Reeside 1938; USGS DB (lateCAM); lots of pubs say it's broadly equiv to Fox Hills = MAA; Finn 2010 (MAA); Farquharson & Grotbo 1981 (CAM/MAA)
MT	Marias River Sh	CEN-SAN	Wallace et al. 1990 (TUR-SAN); USGS DB (CEN-SAN); Farquharson & Grotbo 1981 (TUR-SAN); Dyman et al. 1996 (CEN/TUR); McMannis 1965 (upper Coloradan = lowest 1/3 of LateCret); Rice & Cobban 1977 (CEN-SAN); Macrostrat (CEN-SAN); Nielsen 2008 (TUR-SAN); Cobban et al. 2005 (CON/SAN in part); Cobban et al. 1959 (CEN-SAN); Landman 1994 (contains CON/SAN ammonites); Cobban 1990 (<i>Sciponoceras gracile</i> from SAN portion); Fuentes et al. 2011 (CEN-SAN); Mudge & Sheppard 1968 (CEN-SAN); Rice 1980 (into the SAN); Jinnah et al. 2009 (CON/SAN at least in part); COSUNA (CEN-SAN)

MT	Kevin Mbr (Marias Riv Sh)	CON/SAN	Wallace et al. 1990 (CON/SAN); Farquharson & Grotbo 1981 (CON/SAN & equiv to Niobrara Chk); Rice & Cobban 1977 (CON/SAN); Wallace et al. 1990 (lowSAN); Macrostrat (CON/SAN); Nielsen 2008 (CON/SAN); Cobban et al. 2005 (CON/SAN in part); Cobban et al. 1959 (CON/SAN); Vuke 2000 (CON/SAN); Mudge & Sheppard 1968 (CON/SAN); Rice 1980 (into SAN); COSUNA (CON/SAN)
MT	Ferdig Mbr (Marias Riv Sh)	TUR	Wallace et al. 1990 (TUR/CON); USGS DB (mid/lateTUR); Farquharson & Grotbo 1981 (TUR/CON & equiv to Carlile Sh); Rice & Cobban 1977 (TUR); Macrostrat (TUR); Nielsen 2008 (TUR); Cobban et al. 1959 (TUR); Vuke 2000 (TUR); Mudge & Sheppard 1968 (TUR); COSUNA (TUR)
MT	Cone Mbr (Marias Riv Sh)	CEN/TUR	Wallace et al. 1990 (TUR); USGS DB (upCEN/lowTUR); Farquharson & Grotbo 1981 (TUR & equiv to Greenhorn Lmst); Rice & Cobban 1977 (CEN/TUR); Macrostrat (CEN/TUR); Nielsen 2008 (TUR); Cobban et al. 1959 (TUR); Vuke 2000 (CEN); Mudge & Sheppard 1968 (TUR); COSUNA (CEN/TUR)
MT	Flowerree Mbr (Marias Riv Sh)	CEN	Farquharson & Grotbo 1981 (TUR & equiv to Mosby Mbr/Greenhorn Lmst); Rice & Cobban 1977 (CEN); Wallace et al. 1990 (CEN); Macrostrat (CEN); Eicher 1967 (upCEN); Cobban et al. 1959 (CEN); Vuke 2000 (CEN); Mudge & Sheppard 1968 (CEN); COSUNA (CEN)
MT	Mowry Sh	ALB/CEN	UMPC strat chart (ALB/CEN); Condon 2000 (lowCEN); USGS DB (lowCEN); Farquharson & Grotbo 1981 (ALB); Dyman et al. 1996 (lowCEN); Rice & Cobban 1977 (ALB); Macrostrat (APT-CEN "Sh", ALB/CEN "Fm"); Cobban & Larson 1997 (lowCEN); Oboh-Ikuenobe et al. 2007 (ALB/CEN); COSUNA (ALB)
MT	Montana Grp	SAN-MAA	Heaton 1950 (SAN-MAA in WY); USGS DB (upSAN-lowMAA); Asquith 1970 (SAN-MAA in WY); Macrostrat (TUR-Thaneitan); UMPC strat chart (SAN/CAM); COSUNA (SAN-MAA)
MT	Niobrara Chk	CON-CAM	Shurr et al. (CON-CAM); UMPC strat chart (CON/SAN); Farquharson & Grotbo 1981 (CON/SAN); Cobban & Larson 1997 (upCON-lowCAM); Nielsen 2008 (CON/SAN); Rice 1980 (into SAN); Jinnah et al. 2009 (CON-CAM); Krystinik & DeJarnett 1995 (into lowCAM); COSUNA (CON/SAN)
MT	Smoky Hills Chk (Niobrara Chk)	SAN/CAM	Shurr et al. (SAN/CAM)
MT	Ft Hays Lmst (Niobrara Chk)	CON	Shurr et al. (CON)

MT	Pierre Sh	CAM/MAA	Stephenson & Reeside 1938 (CAM/MAA in Great Plains); Tibert et al. 2009 (CAM/MAA in northern Plains); USGS DB (CAM/MAA); Asquith 1970 (SAN/CAM in WY); Hicks et al. 1995 (CAM/MAA in WY); He et al. 2005 (CAM/MAA); Macrostrat (CON-MAA "Fm" or SAN-MAA "Sh Fm"); UMPC strat chart (CAM); Farquharson & Grotbo 1981 (SAN at least to start); Nielsen 2008 (CAM); Rice 1980 (CAM)
MT	Crow Crk Mbr Pierre Sh	CAM	Shurr et al. 1994 (CAM); USGS DB (CAM); Asquith 1970 (CAM)
MT	De Grey Mbr Pierre Sh	CAM	Shurr et al. 1994 (CAM); USGS DB (upCAM); Asquith 1970 (CAM)
MT	Gammon Sh (= Gammon Ferruginous Mbr) (Pierre Sh)	CAM (low)	Condon 2000 (lowCAM); USGS DB (lowCAM); Cobban & Larson 1997 (lowCAM); Rice 1980 (lowCAM); Krystinik & DeJarnett 1995 (low/midCAM)
MT	Grand SS bed Gammon Sh Pierre Sh		Rice 1980 ("Groat SS bed" is lowCAM...)
MT	Gregory Mbr Pierre Sh	CAM	Shurr et al. 1994 (CAM); USGS DB (CAM); Asquith 1970 (CAM)
MT	Mobridge Mbr Pierre Sh	MAA	Shurr et al. 1994 (MAA); USGS DB (MAA); Asquith 1970 (MAA)
MT	Sharon Springs Sh Pierre Sh	CAM	Shurr et al. 1994 (CAM); USGS DB (CAM); Asquith 1970 (CAM)
MT	Virgin Crk Mbr Pierre Sh	CAM	Shurr et al. 1994 (CAM); USGS DB (CAM); Asquith 1970 (CAM)
MT	Verendrye Mbr Pierre SH	CAM	Shurr et al. 1994 (CAM); USGS DB (CAM); Asquith 1970 (CAM)
MT	St. Mary River Fm	MAA	Roberts et al. 2005 (MAA); Lockley et al. 2003 (MAA in Canada); USGS DB (upMAA); Nadon 1993 (MAA); Rogers & Brady 2010 (MAA); Hunter et al. 2010 (CAM/MAA); Rice & Cobban 1977 (MAA); Bibler 1985 (MAA); Macrostrat (MAA); Farquharson & Grotbo 1981 (CAM/MAA); McMannis 1965 (highest Montanan = upper 1/3 LateCret, but below Lancian which = MAA); Wallace et al. 1990 (upCAM/lowMAA); Fuentes et al. 2011 (CAM/MAA); Mudge & Sheppard 1968 (up-mostCAM/MAA); Rice 1980 (MAA); Scherzer & Varricchio 2010 (MAA); COSUNA (MAA);

			NONMARINE	
MT	Telegraph Creek Fm	SAN/CAM	Heaton 1950 (SAN/CAM); Stephenson & Reeside 1938 (SAN/CAM); Nichols & Sweet 1993 (SAN/CAM); USGS DB (SAN/CAM); Asquith 1970 (SAN/CAM in WY); Rice & Shurr 1980 (shelf ss); Hicks et al. 1995 (CAM in WY); Payenberg et al. 2002 (SAN); Payenberg et al. 2003 (SAN); Robinson et al. 1959 (CAM); Condon 2000 (upSAN/lowCAM); Roger & Brady 2010 (CAM); Landman & Cobban 2007 (SAN); Finn 2010 (CAM); Rice & Cobban 1977 (SAN); Wallace et al. 1990 (SAN); Macrostrat (TUR-CAM); UMPC strat chart (SAN); Farquharson & Grotho 1981 (SAN); McMannis 1965 (lowest Montanan = mid-LateCret); Nielsen 2008 (CAM); Cobban et al. 2005 (upSAN); Cobbn et al. 1959 (SAN); Fuentes et al. 2011 (SAN/CAM); Mudge & Sheppard 1968 (SAN); Rice 1980 (SAN); COSUNA (SAN/CAM)	
MT	Two Medicine Fm	CAM	Bertog et al. 2007 (low/upCAM); Bertog 2002 (midCAM); Farquharson & Grotho 1981 (upSAN/CAM); McMannis 1965 (middle Montanan = middle/upper 1/3 LateCret); Naddon 1993 (CAM); Rice & Cobban 1977 (CAM); Rogers et al. 2010 (CAM); Wallace et al. 1990 (CAM); USGS DB (CAM); Macrostrat (SAN-MAA); Fuentes et al. 2011 (CAM); Mudge & Sheppard 1968 (CAM); Rice 1980 (CAM); Oheim 2007 (CAM); Scherzer & Varricchio 2010 (CAM); Jinnah et al. 2009 (CAM); Krystinik & DeJarnett 1995 (CAM); COSUNA (CAM/lowestMAA); NONMARINE	
MT	Virgelle SS	SAN/CAM	Wallace et al. 1990 (upSAN); Farquharson & Grotho 1981 (SAN/lowCAM); McMannis 1965 (Montanan just above Telegraph Crk = low middle 1/3 LateCret); Payenberg et al. 2002 (CAM in Southern MT, SAN in Alberta); Payenberg et al. 2003 (SAN in MT/Alberta); Rice & Cobban 1977 (SAN); USGS DB (lowCAM); Macrostrat (SAN/CAM); Fuentes et al. 2011 (CAM); Mudge & Sheppard 1968 (CAM); Rice 1980 (SAN/lowCAM); Scherzer & Varricchio 2010 (CAM); Hancock 1993 (lowCAM); Heaton 1950 (SAN); Jinnah et al. 2009 (lowCAM); Krystinik & DeJarnett 1995 (lowCAM); COSUNA (SAN/CAM)	
MT	Warm Creek Sh		Stephenson & Reeside 1938 (TUR-SAN)	

MT	Willow Creek Fm	MAA+	USGS DB (MAA+); Nadon 1993 (MAA including KT boundary); Hunter et al. 2010 (MAA); Russell 1950 (MAA+); Jerzykiewicz 1992 (MAA+); Lehman 1987 (MAA); McMannis 1965 (MAA+); Constenius 1996 (MAA+); Mack & Cole 2005 (MAA+); Rice & Cobban 1977 (MAA+); Macrostrat (MAA-Thaneian); Farquharson & Grotho 1981 (MAA to start); McMannis 1965 (Lancian+ = MAA+); Fuentes et al. 2011 (CAM/MAA); Mudge & Sheppard 1968 (up-most CAM/MAA+); Rice 1980 (MAA+); COSUNA (MAA+); NONMARINE
NE	Carlile Sh	TUR	Joeckel et al. 2004; Hattin 1986 (general WIS); Shurr et al. 1994; Stephenson & Reeside 1938 (TUR in Great Plains); Macrostrat (TUR-CON); COSUNA (TUR)
NE	Dakota Grp	ALB/CEN	COSUNA (ALB/CEN)
NE	Fox Hills SS	MAA	Kennedy et al. 1998; Stephenson & Reeside 1938 (MAA in Great Plains); Macrostrat (CAM/MAA)
NE	Graneros Sh	CEN/TUR	Joeckel et al. 2004 (CEN); Hattin 1986 (general WIS); Shurr et al. 1994 (CEN); Stephenson & Reeside 1938 (CEN/TUR in Great Plains); Macrostrat (CEN); COSUNA (CEN)
NE	Greenhorn Lmst	CEN/TUR	Joeckel et al. 2004 (CEN/TUR); Arratia & Chorn 1998 (TUR); Hattin 1986 (general WIS); Shimada et al. 2009 (CEN/TUR); Shurr et al. 1994 (CEN/TUR); Stephenson & Reeside 1938 (CEN/TUR in Great Plains); Macrostrat (CEN/TUR); COSUNA (CEN/TUR)
NE	Niobrara Chk	CON-CAM	Hattin 1986 (general WIS); Shurr et al. 1994; Stephenson & Reeside 1938 (CON/SAN in Great Plains); Macrostrat (CEN-SAN); COSUNA (TUR-SAN in part)
NE	Pierre Sh	CAM/MAA	Izett 1998 (CAM Crow Creek Mbr/Pierre in SD/NE); Hattin 1986 (CAM general WIS); Diffendal & Flowerday 1995 (CAM/lowestMAA in KS, NE, SD); Shurr et al. 1994; Stephenson & Reeside 1938 (CAM/MAA in Great Plains); Macrostrat (CON-MAA "Fm" or SAN-MAA "Sh Fm"); COSUNA (CAM in part)
NM	Atarque SS	TUR	Hook & Cobban 2007 (TUR); Mack 1987 (TUR); USGS DB (TUR); Mack 1992 (TUR); Wolberg 1985a,b (TUR); Kirkland et al. 2005 (<i>Collignonicerias woolgari</i> zone = midTUR); Spielman & Lucas 2006 (TUR); Charmberlain et al. 1994 (TUR); Shanley & McCabe 1995 (midTUR); Molenaar 1983 (TUR); Irby 1995 (low/midTUR)
NM	Beartooth Quartzite	ALB/CEN	Mack 1987 (ALB/CEN); Chafetz 1982 (early/midCEN - equiv to early Dakota SS); Lucas & Lawton 2005 (CEN Beartooth); Cobban et al. 2008 (lowCEN); Gorrell 1958 (ALB/CEN); Macrostrat (ALB/CEN "Fm"); Molenaar 1983

				(CEN); COSUNA (ALB/CEN); most papers say is equiv to lower Mancos
NM	Carlile Sh	TUR		Hattin 1986 (TUR); Merewether et al. 2007 (mid/upTUR); Young 1960 (TUR); Macrostrat (TUR or CEN-CON); Ridgeley 2000 (TUR); COSUNA (TUR); Campbell 1971 (TUR); USGS DB (TUR/SAN); Bratt 1993 (midTUR Fairport Sh, Blue Hill, Codell mbrs of Carlile)
NM	Cliff House SS	CAM		Campbell 1971 (CAM); Donselaar 1989 (CAM); Palmer & Scott 1984 (CAM); Williamson 1996 (CAM); Williamson et al. 2009 (CAM); Wright 1986 (CAM); Cobban 1973 (CAM); Sixsmith et al. 2008 (CAM); Ridgeley 2000 (CAM); Molenaar 1983 (CAM); Martinsen 2003 (lowCAM); Nummedal & Molenaar 1995 (CAM); Jennette & Jones 1995 (CAM); COSUNA (CON)
NM	Crevasse Canyon Fm	CON		Hook & Cobban 2007; Hook 2010 (mid); Williamson et al. 2009 (TUR/CON); Sixsmith et al. 2008 (TUR/CON); Chamberlain et al. 2008 (CON/SAN); Mack 1992 (SAN/CAM); USGS DB (CON/SAN); Kirkland et al. 2005 (TUR/CON); Chamberlain et al. 1994 (TUR-SAN?); Macrostrat (TUR/CON); Ridgeley 2000 (TUR/CON); Molenaar 1983 (CON/SAN); Jimmah et al. 2009 (CON/lowSAN); Martinsen 2003 (CON-CAM); Cather & Osburn 2007 (CON-SAN?); Nummedal & Molenaar 1995 (TUR-SAN); Jennette & Jones 1995 (CON/SAN); COSUNA (CON); NONMARINE
NM	Dilco Mbr (Crevasse Canyon Fm)	CON		USGS DB (CON, as mbr of Crevasse Canyon or Mesaverde); Chamberlain et al. 2008 (CON "Dilco Coal Mbr" of Crevasse Canyon); Hook 2010 (low/midCON); Ridgeley 2000 (TUR); Nummedal & Molenaar 1995 (TUR); Jennette & Jones 1995 (CON); NONMARINE
NM	Dakota SS/Grp	ALB/CEN		Hattin 1986 (ALB/CEN); Heaton 1950 (CEN); Scott et al. 2004 (ALB/CEN); Campbell 1971 (CEN); Donselaar 1989 (CEN); Hook & Cobban 2007 (CEN Dakota); Wright 1986 (CEN); Sixsmith et al. 2008 (CEN); Chamberlain et al. 2008 (lowCEN); Chamberlain et al. 1994 (CEN); Bratt 1993 (midCEN); Macrostrat (APT-TUR for "Fm/Grp", BERR-TUR for "Grp", ALB/CEN for "SS" in NM); Ridgeley 2000 (CEN); Molenaar 1983 (CEN); Martinsen 2003 (CEN); Nummedal & Molenaar 1995 (CEN at least in part); Jennette & Jones 1995 (CEN at least in part); COSUNA (APT-CEN); Cather & Osburn 2007 (midCEN)
NM	Paguate SS (Dakota SS)	CEN (mid/up)		USGS DB (upper midCEN); Chamberlain 1994 (CEN); Ridgeley 2000 (CEN); Sageman 1996 (mid/upCEN); Lucas & Rinehart 2009 (midCEN); Lucas 2002 (midCEN); Irby 1995 (mid/upCEN); Mellere 1994 (mid/upCEN); Nummedal & Molenaar 1995 (CEN); COSUNA (CEN as Mancos Sh mbr)

NM	Twowells SS (Dakota SS)	CEN (up)	USGS DB (low upCEN); Chamberlain 1994 (upCEN); Hook & Cobban 2007 (CEN); Ridgeley 2000 (CEN/TUR); Sageman 1996 (upCEN); Lucas 2002 (upCEN); Irby 1995 (upCEN); Mellere 1994 (upCEN); Nummedal & Molenaar 1995 (CEN); Nummedal et al. 1993 (mid upCEN); COSUNA (CEN as Mancos Sh mbr)
NM	Fruitland Fm	CAM/MAA	Ambrose & Ayers 2007 (CAM); Heaton 1950 (MAA in NW-NM); Lindsay et al. 1981 (<i>Baculites compressus</i> zone = upCAM); Armstrong-Ziegler 1978 (CAM); Campbell 1971 (MAA); Donselaar 1989 (MAA); Milner et al. 2004 (CAM/MAA); Palmer & Scott 1984 (CAM/MAA); Williamson et al. 2009 (CAM/MAA); Lucas & Mateer 1983 (CAM); Eaton & Kirkland 2008 (upCAM); Roberts et al. 2005 (CAM in coastal plain); Macrostrat (CAM); Ridgeley 2000 (CAM); Molenaar 1983 (CAM/MAA); Jinnah et al. 2009 (upCAM); Martinsen 2003 (CAM); Nummedal & Molenaar 1995 (CAM/MAA); Jennette & Jones 1995 (CAM/MAA); COSUNA (CAM); NONMARINE
NM	Gallup SS	TUR/CON	Campbell 1971 (CON); Donselaar 1989 (CON); Hook & Cobban 2007 (CON); Jennette et al. 1991 (upTUR/lowCON); Hook 2010 (lowCON); Sixsmith et al. 2008 (TUR); Chamberlain et al. 2008 (lowCON); USGS DB (TUR/CON); Mack 1992 (CON/SAN); Molenaar 1974 (TUR/CON); Kirkland et al. 2005 (upTUR); Nummedal et al. 1993 (upTUR/lowCON); Shanley & McCabe 1995 (upTUR); Macrostrat (TUR); Ridgeley 2000 (TUR); Molenaar 1983 (TUR); Martinsen 2003 (TUR/lowestCON); Cather & Osburn 2007 (lowCON); Irby 1995 (upTUR); Nummedal & Molenaar 1995 (TUR); Jennette & Jones 1995 (CEN/TUR); COSUNA (TUR/CON)
NM	Gallego SS (Gallup SS)	TUR/CON	Macrostrat (TUR); COSUNA (TUR/CON)
NM	Graneros Sh	CEN	Hattin 1986 (CEN); Scott et al. 2004 (CEN); USGS DB (CEN); Bratt 1993 (CEN); Macrostrat (CEN); Ridgeley 2000 (CEN/TUR); Nummedal & Molenaar 1995 (CEN); COSUNA (CEN)
NM	Greenhorn Fm	CEN/TUR	Hattin 1986 (CEN/TUR); Merewether et al. 2007 (CEN/TUR); Young 1960 (CEN/TUR); Campbell 1971 (CEN/TUR); USGS DB (CEN/TUR); Spielman & Lucas 2006 (CEN); Bratt 1993 (CEN/TUR); Macrostrat (CEN/TUR); Ridgeley 2000 (CEN/TUR); Molenaar 1983 (TUR); Jennette & Jones 1995 (CEN/TUR); COSUNA (CEN)
NM	Kirtland Fm	CAM/MAA	Ambrose & Ayers 2007 (CAM/MAA); Heaton 1950 (MAA in NW-NM); Campbell 1971 (MAA); Milner et al. 2004 (CAM/MAA); Williamson et al. 2009 (CAM/MAA); Eaton & Kirkland 2008 (upCAM/MAA); Roberts et al. 2005 (CAM in coastal plain); Macrostrat (CAM/MAA); Ridgeley 2000 (CAM/MAA); Molenaar 1983 (CAM/MAA); Jinnah et al. 2009 (upCAM in

			part); Martinsen 2003 (CAM/MAA); Nummedal & Molenaar 1995 (CAM/MAA); Jennette & Jones 1995 (CAM/MAA); COSUNA (CAM/MAA); NONMARINE
NM	Lewis Sh	CAM	Heaton 1950 (MAA in NW-NM); Lindsay et al. 1981 (<i>Didymoceras cheyennense</i> zone = upCAM); Campbell 1971 (CAM); Palmer & Scott 1984 (CAM/MAA); Williamson 1996 (CAM); Williamson et al. 2009 (CAM); Cobban 1973 (CAM); Sixsmith et al. 2008 (CAM); USGS DB (CAM/MAA); Lucas & Mateer 1983 (CAM); Spielman & Lucas 2006 (CAM); Roberts et al. 2005 (midCAM); Macrostrat (CON-CAM); Ridgeley 2000 (CAM); Molenaar 1983 (CAM in CO); Martinsen 2003 (CAM); Nummedal & Molenaar 1995 (CAM); Jennette & Jones 1995 (CAM); COSUNA (SAN)
NM	Mancos Sh/Fm	CEN-CAM	Heaton 1950 (TUR-SAN in NW-NM); Campbell 1971 (TUR-SAN); Wright 1986 (CEN-CAM); Mack 1987 (CEN+); Sixsmith et al. 2008 (CEN-CAM); Macrostrat (CEN-CAM); Ridgeley 2000 (CEN-SAN); Molenaar 1983 (CEN-CAM); Martinsen 2003 (CEN-CAM); COSUNA (CEN-SAN); Young 1960 (TUR begins); Donselaar 1989 (CEN-CAM); Williamson et al. 2009 (CEN-CAM); Palmer & Scott 1984 (into CAM); Williamson 1996 (into SAN); Nummedal & Molenaar 1995 (CEN-CAM); Jennette & Jones 1995 (CEN-CAM); Hook & Cobban 2007 (CEN "lower tongue"); USGS DB (CEN-CAM); Cather & Osburn 2007 (midCEN/lowTUR lower Mancos)
NM	D-Cross Tongue (Mancos Sh)	TUR/CON	Hook & Cobban 2007 (TUR); Hook 2010 (upTUR/lowCON); Cobban et al. 2008 (upTUR); Chamberlin et al. 2008 (midTUR/lowCON); USGS DB (lateTUR); Mack 1992 (CON/SAN); Spielman & Lucas 2006 (TUR); Macrostrat (TUR, CEN-CAM whole Mancos); Ridgeley 2000 (TUR); Cather & Osburn 2007 (midTUR/lowCON); COSUNA (TUR)
NM	La Ventana Tongue (Mancos Sh)	CAM	Palmer & Scott 1984 (CAM); Williamson 1996 (CAM); Wright 1986 (CAM); Ridgeley 2000 (CAM); Molenaar 1983 (CAM); Nummedal & Molenaar 1995 (CAM)
NM	Mulatto Tongue (Mancos Sh)	CON	Hook & Cobban 2007 (CON); Hook 2010 (lowCON); USGS DB; Spielman & Lucas 2006; Kirkland et al. 2005 (CON); Williamson & Lucas 1990 (lowSAN); Macrostrat (CEN-CAM Mancos); Ridgeley 2000 (CON); Molenaar 1983 (CON); Nummedal & Molenaar 1995 (CON)
NM	Pescado Tongue (Mancos Sh)	TUR/CON	USGS DB (TUR); Cobban & Reeside 1952a (TUR); Kirkland et al. 2005 (TUR); Macrostrat (CEN-CAM Mancos); Ridgeley 2000 (TUR); Molenaar 1983 (TUR)

NM	Rio Salado Tongue (Mancos Sh)	TUR	Hook & Cobban 2007 (TUR); Kennedy et al. 2001 (TUR); USGS DB (upCEN/TUR); Spielman & Lucas 2006 (TUR); Kirkland et al. 2005 (TUR); Chamberlain et al. 1994 (CEN/TUR); Macrostrat (CEN-CAM Mancos); Molenaar 1983 (CEN/TUR); Irby 1995 (lowTUR)
NM	Tocito SS Lentil Mbr (Mancos Sh)	CON	Molenaar 1983 (CON); Shanley & McCabe 1995 (low/midCON); Jennette et al. 1991 (CON); Moutoux 2000 (equiv to Mulato Tongue = CON); Ridgely 2000 (TUR); Molenaar 1983 (CON); Valasek 1995 (low/midCON); Elder & Kirkland (CON); Martinsen 2003 (CON); Nummedal & Molenaar 1995 (CON); Jennette & Jones 1995 (TUR/CON); Nummedal et al. 1993 (CON)
NM	Whitewater Arroyo Sh (Mancos Sh)	CEN (mid/up)	USGS DB (mid/upCEN); Chamberlain 1994 (upCEN); Ridgely 2000 (CEN); Lucas 2002 (mid/upCEN); Irby 1995 (upCEN); Mellere 1994 (mid/upCEN); Nummedal & Molenaar 1995 (CEN); COSUNA (CEN)
NM	McRae Fm	MAA	Mack 1992 (MAA); Buck & Mack 1995 (MAA); Seager et al. 1997 (MAA); Lehman 1987 (MAA); Bogner et al. 2007 (MAA); NONMARINE (full of paleosols and dinos)
NM	Menefee Fm	CAM	Campbell 1971 (CAM); Donselaar 1989 (CAM); Palmer & Scott 1984 (CAM); Williamson 1996 (CAM); Wright 1986 (SAN/CAM); Sixsmith et al. 2008 (CAM); USGS DB (SAN); Shanley & McCabe 1995 (CAM); Macrostrat (CON "Fm, CON/SAN "Sh Fm"); Ridgely 2000 (SAN/CAM); Molenaar 1983 (CAM); Jimnah et al. 2009 (low/midCAM); Martinsen 2003 (CAM); Nummedal & Molenaar 1995 (CAM); Jennette & Jones 1995 (CAM); COSUNA (CON); partially, if not mostly, nonmarine
NM	Mesaverde Grp	CON-CAM	Heaton 1950 (SAN/CAM in NW-NM); Campbell 1971 (SAN/CAM); Palmer & Scott 1984 (SAN/CAM); Wright 1986 (SAN/CAM); Cobban 1973 (CAM); USGS DB; Macrostrat (TUR-MAA); Molenaar 1983 (CAM); Martinsen 2003 (TUR-CAM); COSUNA (TUR/CON "Grp" SAN-MAA "Fm"); Nummedal & Molenaar 1995 (CAM); Jennette & Jones 1995 (SAN/CAM); upper 1/2 (Williams Fork Fm) is nonmarine; adding CON because Dalton SS/Mesaverde Grp is CON
NM	Dalton SS (Mesaverde Grp)	CON	USGS DB (CON); Dane et al. 1957 (CON+), Dalton overlies Mulato Tongue/Mancos = CON); Donselaar 1989 (CON); McCubbin 1969 (~ CON, equiv to lower Niobrara = CON, overlies Mullato Tongue = CON, underlies Point Lookout = SAN/CAM); Sixsmith et al. 2008 (CON/SAN); Spielman & Lucas 2006 (midCON); Shanley & McCabe 1995 (upCON); Valasek 1995 (upCON); Moutoux 2000 (SAN); Ridgely 2000 (CON); Edwards et al. 2005 (equiv to Emery SS in UT = SAN); Molenaar 1983 (CON/SAN); Shanley & McCabe 1995 (lowSAN); Nummedal & Molenaar 1995 (SAN); some pubs say Dalton SS is a mbr of the Crevasse Canyon Fm (others say Mesaverde Grp)

NM	Hosta SS Mbr (Dalton SS) (Mesaverde Grp)	SAN	USGS DB (SAN); Donselaar 1989 (CON); McCubbin 1969 (CON/SAN; equiv to mid-NIO = SAN, overlies Dalton SS = CON, underlies Point Lookout = SAN/CAM); Sixsmith et al. 2008 (SAN); Spielman & Lucas 2006 (midSAN); Shanley & McCabe (lowSAN); Valasek 1995 (lowSAN); Moutoux 2000 (SAN); Ridgeley 2000 (CON); Molenaar 1983 (SAN); Nummedal & Molenaar 1995 (CAM); Lucas et al. 2000 (SAN); NOTE: some articles say Hosta SS is a mbr of Point Lookout Fm
NM	Moreno Hill Fm	TUR	Mack 1987 (TUR); USGS DB (mid/lateTUR); Mack 1992 (TUR); Kirkland & Wolfe 2001 (TUR); Wolfe et al. 2010 (TUR); Eaton & Kirkland 2008 (TUR); Sweeney et al. 2009 (TUR); Kirkland et al. 2005 (TUR); Chamberlain et al. 1994 (TUR); Molenaar 1983 (TUR); Irby 1995 (mid/upTUR)
NM	Niobrara Fm	TUR-SAN	Hattin 1986 (CON-CAM); Heaton 1950 (CON/SAN); Macrostrat (CEN-SAN); Ridgeley 2000 (TUR-SAN); COSUNA (TUR-SAN)
NM	Fort Hays (Niobrara Fm)	CON	Hattin 1986 (CON); Heaton 1950 (CON/SAN Niobrara); USGS DB (upTUR/lowCON); Macrostrat (TUR-CON); Schumacher & Everhart 2005 (CON); COSUNA (TUR/CON); other states is predominantly CON
NM	Pictured Cliffs SS	CAM/MAA	Ambrose & Ayers 2007 (upCAM/lowMAA); Heaton 1950 (MAA); Molenaar et al. 2002 (CAM); Lindsay et al. 1981 (CAM); Campbell 1971 (CAM); Donselaar 1989 (CAM/lowMAA); Milner et al. 2004 (CAM); Palmer & Scott 1984 (CAM/MAA); Williamson 1996 (CAM); Williamson et al. 2009 (CAM); Cobban 1973 (CAM); Sixsmith et al. 2008 (CAM); Lucas & Mater 1983; Spielman & Lucas 2006 (CAM); Macrostrat (SAN); Ridgeley 2000 (CAM); Molenaar 1983 (CAM); Jinnah et al. 2009 (upCAM); Martinsen 2003 (upCAM); Nummedal & Molenaar 1995 (CAM); Jennette & Jones 1995 (CAM/MAA); COSUNA (SAN/CAM)
NM	Pierre Sh	CAM/MAA	Hattin 1986 (CAM in part); Heaton 1950 (CAM/MAA); Campbell 1971 (CAM/MAA); Spielman & Lucas 2006 (CAM); Macrostrat (CON-MAA "Fm" or SAN-MAA "Sh Fm"); Ridgeley 2000 (CAM/MAA)
NM	Point Lookout SS	SAN/CAM	Campbell 1971 (SAN/CAM); Donselaar 1989 (SAN/CAM); Palmer & Scott 1984 (up-mostSAN/CAM); Williamson 1996 (SAN/CAM); Williamson et al. 2009 (lowCAM); Wright 1986 (CON-CAM); Cobban 1973 (SAN/CAM); Sixsmith et al. 2008 (SAN/CAM); Spielman & Lucas 2006 (SAN Hosta Tongue/Point Lookout); Shanley & McCabe 1995 (SAN); Macrostrat (TUR-CON); Ridgeley 2000 (SAN); Molenaar 1983 (SAN/CAM, mainly CAM); Martinsen 2003 (lowCAM); Nummedal & Molenaar 1995 (CAM); Jennette & Jones 1995 (SAN/CAM); COSUNA (CON)
NM	Tres Hermanos	TUR	Macrostrat (TUR), Cather & Osburn 2007 (midTUR); Chamberlain et al. 2008 (midTUR); Hook & Cobban 2007 (TUR); Hook 2010 (TUR at least in part - Atarque SS Mbr = TUR); Mack 1992 (TUR); Spielman & Lucas 2006 (TUR);

			Toolson & Kues 1996 (TUR at least in part)	
NM	Trinidad SS	MAA	Heaton 1950 (MAA); Lehman 1987 (MAA); Macrostrat (SAN/CAM); is MAA in CO; NONMARINE	
NM	Vernejo Fm	MAA	Heaton 1950 (MAA); Wolfe & Upchurch 1987 (MAA); Lehman 1987 (MAA); Macrostrat (CAM)	
ND	Belle Fourche Fm	CEN	COSUNA (CEN)	
ND	Carlile Fm	TUR/CON	COSUNA (TUR/CON)	
ND	Colorado Grp	CEN-SAN	COSUNA (CEN-SAN)	
ND	Fox Hills Fm	MAA	Stephenson & Reeside 1938 (MAA in Great Plains); Tibert et al. 2009 (MAA in northern Plains); USGS DB; He et al. 2005 (MAA); Becker et al. 2009 (MAA); Crawford et al. 2006 (MAA); Peppe et al. 2007 (MAA); Wilson 2006 (MAA); Macrostrat (CAM/MAA); COSUNA (MAA)	
ND	Greenhorn Fm	CEN/TUR	COSUNA (CEN/TUR)	
ND	Hell Creek Fm	MAA	Stephenson & Reeside 1938 (DAN in Great Plains); Tibert et al. 2009 (MAA in northern Plains); USGS DB (lowest Paleocene); He et al. 2005; Fox 1971 (MAA in MT); Becker et al. 2009 (MAA); Carlson & Anderson 1965 (MAA); Condon 2000 (lateMAA in MT); Wilson 2006 (MAA); Finn 2010 (MAA in MT); Macrostrat (MAA); COSUNA (MAA); NONMARINE	
ND	Montana Group	SAN-MAA	COSUNA (SAN-MAA)	
ND	Niobrara Chk	CON-CAM	Bertog et al. 2007 (ends lowCAM); COSUNA (CON/SAN)	
ND	Pierre Sh	CAM/MAA	Stephenson & Reeside 1938 (CAM/MAA in Great Plains); Tibert et al. 2009 (CAM/MAA in northern Plains); USGS DB (CAM/MAA); He et al. 2005 (CAM/MAA); Becker et al. 2004 (into MAA); Hanczaryk & Gallagher 2007 (CAM); Patrick et al. 2004 (CAM/MAA); Stoffer 2003 (CAM/MAA); Bishop 1985 (CAM/MAA); Macrostrat (CON-MAA "Fm" or SAN-MAA "Sh Fm"); Bertog 2010 (CAM to start); COSUNA (SAN-MAA)	
ND	Sharon Springs Sh (Pierre Sh)	CAM	Bertog 2010 (low/midCAM)	
ND	Gregory Mbr (Pierre Sh)	CAM (mid)	Shurr et al. 1994 (CAM in SD); Bertog et al. 2007 (midCAM in Black Hills); Hanczark & Gallagher 2007 (midCAM in SD); Patrick et al. 2007 (midCAM in SD); Bertog 2010 (midCAM)	

OK	Brownstown Marl	SAN/CAM	Akers & Akers 1997 (SAN in TX); USGS DB (CAM); Emerson et al. 1994 (CAM in N TX); Hazel & Paulson 1964 (CAM in northeast TX); Macrostrat (SAN/CAM for "Fm" ...CAM/MAA for "Marl" ...); Mancini & Puckett 2005 (low/midCAM in NW Gulf); Waggoner 2006 (lowCAM in Gulf region)
OK	Caddo Fm	ALB	Tappan 1943 (ALB); Huffman et al. 1975 (Comanche; equivalent to lower Washita Grp - ALB?); Bullard 1925 (lower Washita Grp just above Kiamichi - ALB/CEN?)
OK	Eagle Ford Fm	CEN/TUR	USGS DB (CEN/TUR); Akers & Akers 1997 (CEN/TUR in TX); Emerson et al. 1994 (CEN/TUR in TX); Ambrose et al. 2009 (CEN/TUR in east TX Basin); Macrostrat (ALB-TUR); Mancini & Puckett 2005 (upCEN/TUR in NW Gulf)
OK	Ozan Fm	CAM	Akers & Akers 1997 (CAM in TX); Emerson et al. (CAM in TX); Clark 2009 (upmostSAN/CAM in TX); Macrostrat (CAM/MAA); USGS DB (LateCret)
OK	Tokio Fm	CON	Benson & Tatro 1964 (also northern LA); Shaw 1967 (CON in AR); Mancini et al. 2008 (CON/SAN in central Gulf Coast); Hazel & Paulson 1964 (CON/SAN in AR); Macrostrat (CON/SAN "Fm" ...TUR-SAN "Tokio Sand Fm" ...); USGS DB (LateCret)
OK	Woodbine Fm	CEN	USGS DB (CEN); Ravn & Witzke 1994 (CEN); Akers & Akers 1997 (CEN in TX); Emerson et al. 1994 (CEN in TX); Ambrose et al. 2009 (CEN in eastern TX Basin); Allmon & Cohen 2008 (CEN in northeast TX); Macrostrat (CEN/TUR); Mancini & Puckett 2005 (mid/upCEN in NW Gulf)
OK	Dexter Mbr (Woodbine Fm)	CEN	USGS DB (CEN); Ravn & Witzke 1994 (CEN Woodbine); Emerson et al. 1994 (CEN in N TX); Ambrose et al. 2009 (CEN in east TX Basin); Allmon & Cohen 2008 (lowCEN in northeast TX); Macrostrat (CEN); Mancini & Puckett 2005 (mid/upCEN Woodbine in NW Gulf)
OK	Lewisville Mbr (Woodbine Fm)	CEN	USGS DB (CEN); Ravn & Witzke 1994 (CEN Woodbine); Emerson et al. 1994 (CEN in N TX); Ambrose et al. 2009 (CEN in east TX Basin); Allmon & Cohen 2008 (lowCEN in northeast TX); Macrostrat (CEN); Mancini & Puckett 2005 (mid/upCEN Woodbine in NW Gulf)
OK	Red Branch Mbr (Woodbine Fm)	CEN	USGS DB (CEN); Ravn & Witzke 1994 (CEN Woodbine); Mancini & Puckett 2005 (mid/upCEN Woodbine in NW Gulf)
OK	Templeton Mbr (Woodbine Fm)	CEN	USGS DB (CEN); Ravn & Witzke 1994 (CEN Woodbine); Emerson et al. 1994 (CEN in N TX); Allmon & Cohen 2008 (lowCEN in northeast TX); Mancini & Puckett 2005 (mid/upCEN Woodbine in NW Gulf)
SD	Belle Fourche Fm	CEN	Kirkland et al. 1999 (CAN); Tibert et al. 2009 (CEN in northern Plains); Yang & Miall 2009 (CEN in northern Great Plains); USGS DB (CEN); Cadrin et al. 1995 (CEN in ND & Canada); Macrostrat (CEN "Sh", ALB/CEN "Fm"); Cobban & Larson 1997 (low/midCEN); Hancock 2004 (low/midCEN); COSUNA (ALB/CEN); Condon 2000 (CEN)

SD	Carlile Sh	TUR	Kirkland et al. 1999 (TUR); Stephenson & Reeside 1938 (TUR in Great Plains); Tibert et al. 2009 (TUR in northern Plains); Yang & Miall 2009 (TUR in northern Great Plains); USGS DB (TUR-SAN); Condon 2000 (TUR in MT); Cadrin et al. 1995 (TUR in ND); Shurr et al. 1994 (TUR); Macrostrat (TUR or CEN-CON); Cobban & Larson 1997 (mid/upTUR); COSUNA (TUR/CON)
SD	Blue Hill Sh (Carlile Sh)	TUR	Shurr et al. 1994 (TUR); Sethi & Leithold 1997 (midTUR in part in CO)
SD	Codell SS (Carlile Sh)	TUR	Shurr et al. 1994 (TUR)
SD	Fairport Chk (Carlile Sh)	TUR	Shurr et al. 1994 (TUR); Sethi & Leithold 1997 (midTUR in CO)
SD	Un-named Mbr (Carlile Sh)	TUR	Hattin 1986 (upTUR); Shurr et al. 1994 (TUR)
SD	Mowry Sh	ALB/CEN	Kirkland et al. 1999 (ALB/CEN); Heaton 1950 (CEN); Stephenson & Reeside 1938 (CEN Mowry in MT); Tibert et al. 2009 (CEN in northern Plains); Yang & Miall 2009 (ALB/CEN in northern Great Plains); USGS DB (CEN); Condon 2000 (CEN in MT); Dutton 1997 (ALB); Cadrin et al. 1995 (CEN in ND & Canada); Finn 2010 (ALB/CEN); Macrostrat (APT-CEN "Sh/CO Grp", ALB-CEN "Fm/CO Grp"); Cobban & Larson 1997 (lowCEN)
SD	Newcastle SS	ALB	Kirkland et al. 1999 (ALB); Heaton 1950 (CEN); USGS DB (ALB); Dutton 1997 (ALB); Cadrin et al. 1995 (ALB in ND & Canada); Finn 2010 (equiv to Muddy SS = ALB); Macrostrat (ALB); COSUNA (ALB)
SD	Fox Hills SS	MAA	Stephenson & Reeside 1938 (MAA in Great Plains); Tibert et al. 2009 (MAA in northern Plains); USGS DB (MAA); Cobban & Kennedy 1992 (MAA); Becker et al. 2004 (MAA); Stoffer 2003 (MAA/Paleocene); Crawford et al. 2006 (MAA); Bishop 1985 (MAA); Macrostrat (CAM/MAA); Cobban & Larson 1997 (upCAM/lowMAA); COSUNA (MAA)
SD	Dakota Fm	ALB/CEN	Shurr et al. 1994 (ALB/CEN); COSUNA (ALB/APT)
SD	Graneros Sh	CEN	Shurr et al. 1994 (CEN); COSUNA (CEN)
SD	Greenhorn Fm	CEN/TUR	Kirkland et al. 1999 (CEN/TUR); Stephenson & Reeside 1938 (TUR in Great Plains); Tibert et al. 2009 (CEN/TUR in northern Plains); Yang & Miall 2009 (TUR in northern Great Plains); USGS DB (CEN/TUR); Condon 2000 (CEN/TUR in MT); Cadrin et al. 1995 (CEN/TUR in ND); Macrostrat (CEN/TUR); Shurr et al. 1994 (CEN/TUR); Cobban & Larson 1997 (upCEN/lowTUR); COSUNA (CEN/TUR)

SD	Hell Creek Fm	MAA	Stephenson & Reeside 1938 (DAN In Great Plains); USGS DB (lowest Paleocene); He et al. 2005 (MAA); Fox 1971 (MAA in MT); Condon 2000 (lateMAA in MT); Finn 2010 (MAA in MT); Macrostrat (MAA); COSUNA (MAA); NONMARINE
SD	Niobrara Chk/Fm	CON-CAM	Stephenson & Reeside 1938 (CON/SAN in Great Plains); Tibert et al. 2009 (CON-CAM in northern Plains); USGS DB (TUR-CAM); Becker et al. 2009 (CON-CAM); Condon 2000 (CON/SAN in MT); Bishop 1985 (top Niobrara = SAN/lowCAM); Macrostrat (CEN-SAN); Cobban & Larson 1997 (upCON-lowCAM); COSUNA (CON/SAN); Shurr et al. (CON-CAM); Bertog 2010 (lowCAM at top)
SD	Smoky Hills Chk (Niobrara Chk)	SAN/CAM	Shurr et al. (SAN/CAM); COSUNA (CON/SAN for Niobrara Fm)
SD	Pierre Sh	CAM/MAA	Stephenson & Reeside 1938 (CAM/MAA in Great Plains); Tibert et al. 2009 (CAM/MAA in northern Plains); USGS DB (CAM/MAA); He et al. 2005 (CAM/MAA); Becker et al. 2004 (into MAA); Hanczaryk & Gallagher 2007 (CAM); Patrick et al. 2004 (CAM/MAA); Stoffer 2003 (CAM/MAA); Bishop 1985 (CAM/MAA); Macrostrat (CON-MAA "Fm" or SAN-MAA "Sh Fm"); Bertog 2010 (CAM to start); COSUNA (CAM/MAA)
SD	Crow Crk Mbr (Pierre Sh)	CAM	Shurr et al. 1994 (CAM); Hanczark & Gallagher 2007 (upCAM); Patrick et al. 2007 (midCAM); USGS DB (CAM)
SD	De Grey Mbr (Pierre Sh)	CAM (up)	Hanczark & Gallagher 2007 (upCAM); Patrick et al. 2007 (upCAM); USGS DB (upCAM)
SD	Gammon Ferruginous Mbr (Pierre Sh)	CAM (low)	Bishop 1985 (lowCAM); Bertog et al. 2007 (low/midCAM in Black Hills); Bertog 2010 (lowCAM); Bertog 2002 (low/midCAM); USGS DB (lowCAM); Cobban & Larson 1997 (lowCAM)
SD	Gregory Mbr (Pierre Sh)	CAM (mid)	Shurr et al. 1994 (CAM); Bertog et al. 2007 (midCAM in Black Hills); Hanczark & Gallagher 2007 (midCAM); Patrick et al. 2007 (midCAM); Bertog 2010 (midCAM); Bertog 2002 (midCAM); USGS DB (CAM)
SD	Kara Bentonitic Mbr (Pierre Sh)	CAM (up)	Bishop 1985 (up-mostCAM)
SD	Mitten Black Sh (Pierre Sh)	CAM	Bishop 1985 (midCAM); Bertog et al. 2007 (midCAM in Black Hills); Bertog 2010 (midCAM); Bertog 2002 (midCAM); Cobban & Larson 1997 (midCAM)
SD	Mobridge Mbr (Pierre Sh)	MAA	Shurr et al. 1994 (MAA); USGS DB (MAA)
SD	Monument Hill Bentonite	CAM	Bishop 1985 (mid/upCam); Cobban & Larson 1997 (upCAM)

	(Pierre Sh)		
SD	Red Bird Silty Mbr (Pierre Sh)	CAM	Bishop 1985 (midCam); Bertog et al. 2007 (midCAM in Black Hills); Bertog 2010 (midCAM); Bertog 2002 (midCAM); Cobban & Larson 1997 (midCAM)
SD	Sharon Springs Sh (Pierre Sh)	CAM	Shurr et al. 1994 (CAM); Bertog et al. 2007 (midCAM in Black Hills); Bertog 2010 (midCAM); Bertog 2002 (midCAM); USGS DB (CAM)
SD	Verendrye Mbr (Pierre Sh)	CAM (up)	Hanczark & Gallagher 2007 (upCAM); Patrick et al. 2007 (upCAM); USGS DB (CAM)
SD	Virgin Crk Mbr (Pierre Sh)	CAM	Shurr et al. 1994 (CAM); USGS DB (CAM)
SD	Skull Creek Sh	ALB	Kirkland et al. 1999 (ALB); Heaton 1950 (CEN); Tibert et al. 2009 (ALB in northern Plains); Yang & Miall 2009 (ALB in northern Great Plains); USGS DB (ALB); Condon 2000 (ALB in MT); Dutton 1997 (ALB); Cadrin et al. 1995 (ALB in ND/Canada); Macrostrat (HAUT-ALB, mostly ALB); COSUNA (ALB/APT)
TN	Coffee Sand	CAM	Harrison & Litwin 1997 (CAM); Kennedy & Cobban 1991 (CAM in MS); Macrostrat (SAN/CAM); COSUNA (in the middle of the "TUR-SAN" bin)
TN	Eutaw Fm	SAN/CAM	Macrostrat (CON-CAM); Mancini & Puckett 2005 (CON/SAN in NE Gulf); COSUNA (in the middle of the "TUR-SAN" bin); and see papers pertaining to AL/MS with these fm's
TN	Owl Crk Fm	MAA	Macrostrat (MAA); and see papers pertaining to AL/MS with these fm's
TN	Coon Creek Tongue (Ripley Fm)	CAM/MAA	Vermeij & Dudley 1982 (CAM/MAA); Heydari 2001 (MAA in MS); Kennedy et al. 2000 (CAM); Macrostrat (MAA); Cobban & Kennedy 1993 (CAM/MAA); COSUNA (CAM)
TN	McNairy Sand (Ripley Fm)	MAA	Heydari 2001 (MAA); Macrostrat (MAA); Harrison & Litwin 1997 (MAA in MS); Heydari 2000, 2001 (MAA in MS); Case & Schwimmer 1988 (MAA in MS); Mancini & Puckett 2005 (upCAM/lowMAA Ripley in NE Gulf); COSUNA (MAA)
TN	Tuscaloosa Fm	CEN-CON	Kennedy & Cobban 1991 (upCEN Tuscaloosa Grp in AL/MS); Macrostrat (CEN-SAN); Mancini & Puckett 2005 (midCEN/TUR Tuscaloosa Fm in NE Gulf); COSUNA (CEN); and see papers pertaining to AL/MS with these fm's
TX	Anacacho Lmst	CAM	Emerson et al. 1994; Akers & Akers 1997; Cobban et al. 2008 (upCAM); Swezey & Sullivan 2004 (CAM); Elder 1996; Kennedy & Cobban 2001 (midCAM); Macrostrat (SAN/CAM "Imst, CAM "Fm"); Hancey 1987 (CAM); Elder 1996 (low/midCAM); COSUNA (CAM)

TX	Aguja Fm	CAM/MAA	Emerson et al. 1994 (CAM); Akers & Akers 1997 (SAN/CAM); Rowe et al. 1992 (CAM); Cobban et al. 2008 (CAM); Wagner & Lehman 2009 (CAM); Longrich et al. 2010 (CAM/MAA for upper sh); Horton 2006 (CAM/MAA); Erdlac Jr. 1990 (CAM); Ashmore 2003 (CAM/MAA); Lehman 1989a (MAA in Brewster Co, TX); Lehman 1985 (in Tomillo Basin, TX = CAM); Wagner 2001 (CAM/MAA Big Bend region); Lehman 2010 (CAM in Brewster Co); Roberts et al. 2005 (upCAM); Macrostrat (CAM/MAA); Hency 1987 (CAM/MAA); Waggoner 2006 (CAM/MAA); Jinnah et al. 2009 (SAN-midCAM); COSUNA (CAM-MAA)
TX	Austin Chk	CON-CAM	Barrier 1980 (CON-CAM); Emerson et al. 1994 (SAN); Mancini et al. 2008 (CON/SAN Austin Grp for Wm Gulf Coast); Akers & Akers 1997 (CON); Alshuaibi 2006 (CON-lowest CAM); Gale et al. 2008 (up-mostTUR-lowestCAM); Cobban et al. 2008 (CAM "Fm"); Elder 1996 (SAN/CAM "Grp"); Trevino et al. 2007 (top = lowCAM in Rio Grande/central TX); Marks & Stam 1983; Young 1986; Ambrose et al. 2009 (CON+); Stephenson & Reeside 1938 (CON/SAN); Clark 2009 (CON/SAN); Macrostrat (TUR-CAM); Mancini & Puckett 2005 (midCON-lowCAM in NW Gulf); Corbett et al. 1987 (CON/SAN); Hency 1987 (CON-CAM); Brown & Pierce 1962 (CON-CAM = "Austinian"); COSUNA (TUR-CAM)
TX	Atco Mbr (Austin Chk)	CON	Barrier 1980 (CON/SAN); Marks & Stam 1983 (CON/SAN); Akers & Akers 1997 (CON); Emerson et al. 1994 (CON); Young 1986 (mid/upCON); USGS DB (CON/SAN = early "Austinian"); Macrostrat (CON); Hency 1987 (CON); Kennedy et al. 2004 (CON); COSUNA (TUR/CON)
TX	Big House (= Pflugerville Mbr) (Austin Chk)	CAM	Barrier 1980 (SAN); Marks & Stam 1983 (SAN Big House); Akers & Akers 1997 (SAN Pflugerville); Emerson et al. 1994 (CAM); Young 1986 (lowCAM); Macrostrat (CAM Pflugerville); Beikirch & Feldmann 1980 (lowCAM Pflugerville); COSUNA ("Pelungerville Fm" = CAM)
TX	Burditt Marl (Austin Chk)	SAN/CAM	Barrier 1980 (SAN); Hazel & Paulson 1964 (CAM); Marks & Stam 1983 (SAN); Akers & Akers 1997 (SAN); Emerson et al. 1994 (CAM); Young 1986 (lowCAM); Macrostrat (SAN); Swezey & Sullivan 2004 (lowCAM); Young & Marks 1952 (SAN); Hency 1987 (CAM); Ross & Maddocks 1983 (CAM); Beikirch & Feldmann 1980 (CAM); COSUNA (SAN/CAM)
TX	Dessau Mbr (Austin Chk)	SAN	Barrier 1980 (SAN); Hazel & Paulson 1964 (SAN/CAM); Marks & Stam 1983 (SAN); Akers & Akers 1997 (CON/SAN boundary); Emerson et al. 1994 (SAN); Young 1986 (upSAN/lowCAM); USGS DB (SAN/CAM = late "Austinian"); Macrostrat (SAN); Hency 1987 (SAN/CAM); Ross & Maddocks 1983 (SAN/CAM); Beikirch & Feldmann 1980 (CAM); Kennedy et al. 2004 (mostly upSAN); Waggoner 2006 (upSAN); COSUNA (SAN)

TX	Jonah Lmst (Austin Chk)	SAN	Barrier 1980 (SAN); Marks & Stam 1983 (SAN); Akers & Akers 1997 (CON); Emerson et al. 1994 (SAN); Young 1986 (lowSAN); USGS DB (late "Austinian" = SAN/CAM); Macrostrat (SAN); Hency 1987 (CON/SAN); Kennedy et al. 2004 (midSAN); COSUNA (SAN)
TX	San Martine Mbr (Boracho Lmst)	ALB	Emerson et al. 1994 (ALB Boracho); Akers & Akers 1997 (ALB)
TX	Vinson Chk (Austin Chk)	CON/SAN	Barrier 1980 (SAN); Marks & Stam 1983 (CON); Akers & Akers 1997 (CON); Emerson et al. 1994 (SAN); Young 1986 (lowSAN); USGS DB (mid "Austinian" = SAN?); Macrostrat (SAN); Hency 1987 (CON); Kennedy et al. 2004 (upCON/lowSAN); COSUNA (SAN)
TX	Buda Lmst	CEN	Kues 1989 (lowCEN); Tappan 1943 (ALB); Barrier 1980 (CEN); Emerson et al. 1994 (CEN); Mancini et al. 2008 (lowCEN in Wrn Gulf Coast); Akers & Akers 1997 (CEN); Cobban et al. 2008 (CEN); Huffman 1960 (lowCEN); Getzender 1930 (CEN); Imlay 1945 (CEN); Young 1986 (lowCEN); Ambrose et al. 2009 (CEN); Allmon & Cohen 2008 (lowCEN); Clark 2009 (CEN); Macrostrat (CEN); Hopkins et al. 1999 (CEN); Scott 1977 (CEN); Mancini & Puckett 2005 (lowCEN in NW Gulf); Hency 1987 (CEN); COSUNA (CEN); Powell 1965 (CEN); Erdlac Jr. 1990 (CEN)
TX	Blossom Sand	SAN	Emerson et al. 1994 (CAM); Akers & Akers 1997 (SAN); Kennedy et al. 2001 (latest SAN); Hazel & Paulson 1964 (SAN); Macrostrat (SAN); Hency 1987 (CON/SAN); Waggoner 2006 (upSAN); COSUNA (SAN)
TX	Bonham Fm	CON/SAN	Alshuaibi 2006 (SAN & same age Bruceville Mbr/Austin Chk); Kennedy et al. 2001 (SAN); Hazel & Paulson 1964 (CON/SAN); Macrostrat (CON/SAN); Hency 1987 (CON)
TX	Boquillas Fm	CEN/TUR	Barrier 1980; Emerson et al. 1994; Akers & Akers 1997; Cobban et al. 2008 (CEN-SAN); Powell 1965 (CEN/TUR); Young 1958 (CEN/TUR); Erdlac Jr. 1990 (CEN/TUR); Huffman 1960 (CEN/TUR); Ashmore 2003 (TUR/CON); Lehman 1985 (CEN-lowCAM for Boquillas + Pen Fm's); Wagner 2001 (CEN-SAN "Boquillas Flags" Big Bend region); Macrostrat (CEN-CAM); Hency 1987 (CEN-SAN); Jinnah et al. 2009 (TUR/CON); COSUNA (CEN-CAM, San Vicente Mbr = TUR-CAM)
TX	Corsicana Marl	MAA	Barrier 1980 (MAA); Emerson et al. 1994 (MAA); Akers & Akers 1997 (MAA); Mancini et al. 2008 (MAA in Wrn Gulf Coast); Swezey & Sullivan 2004 (MAA); Elder 1996 (upMAA); Kennedy & Cobban 1993 (MAA); Trevino et al. 2007 (upMAA); Young 1986 (low/midMAA); Stephenson & Reeside 1938 (MAA); Clark 2009 (MAA); Mancini & Puckett 2005 (MAA); Hancock 1993 (upMAA); Hency 1987 (MAA)
TX	Dakota Fm	CEN	Macrostrat (APT-TUR for "Fm/Grp", BERR-TUR for "Grp"); most other states is CEN

TX	Del Rio Clay	CEN	Tappan 1943 (ALB); Barrier 1980 (ALB/CEN); Akers & Akers 1997 (CEN); Cobban et al. 2008 (lowCEN); Erdlac Jr. 1990 (CEN); Getzendaner 1930 (CEN); Young 1986 (lowCEN); Allmon & Cohen 2008 (lowCEN); Macrostrat (ALB/CEN); Scott 1977 (CEN); Hency 1987 (CEN); COSUNA (ALB/CEN); Emerson et al. 1994 (CEN)
TX	Eagle Ford Fm	CEN/TUR	Barrier 1980 (CEN/TUR); Emerson et al. 1994 (CEN/TUR); Mancini et al. 2008 (upCEN/TUR); Akers & Akers 1997 (CEN/TUR); Myers 2010 (CEN/TUR); Huffman 1960 (CEN/TUR); Young 1986 (CEN/TUR); Ambrose et al. 2009 (CEN/TUR); Allmon & Cohen 2008 (midCEN lower Eagle Ford); Stephenson & Reeside 1938 (CEN/TUR); Kirkland et al. 1999 (CEN/TUR); Clark 2009 (CEN/TUR); Macrostrat (ALB-TUR); Mancini & Puckett 2005 (upCEN/TUR); Dawson 1997 (CEN/TUR); Hency 1987 (CEN-CON); Liro et al. 1994 (CEN/TUR); Brown & Pierce 1962 (CEN/TUR = "Eaglefordian"); Dawson 2000 (CEN/TUR); Christopher 1982 (CEN/TUR); COSUNA (ALB-TUR)
TX	Arcadia Park Mbr (Eagle Ford)	TUR	Huffman 1960 (TUR); Myers 2010 (TUR); Akers & Akers 1997 (TUR); Emerson et al. 1994 (TUR); USGS DB (TUR); Moreman 1942 (upTUR); Dawson 1997 (TUR); Liro et al. 1994 (TUR); Brown & Pierce 1962 (mid/lateTUR); Dawson 2000 (TUR); Christopher 1982 (upTUR)
TX	Britton Clay (Eagle Ford)	CEN/TUR	Allmon & Cohen 2008 (midCEN); Huffman 1960 (CEN/TUR); Myers 2010 (CEN/TUR); Akers & Akers 1997 (CEN/TUR); Emerson et al. 1994 (CEN/TUR); USGS DB (middle upCEN); Moreman 1942 (lowTUR); Dawson 1997 (CEN/TUR); Liro et al. 1994 (CEN/TUR); Brown & Pierce 1962 (upCEN/lowTUR); Bishop et al. 1992 (CEN); Dawson 2000 (CEN/TUR); Christopher 1982 (CEN/lowTUR); Bishop & Brannen 1992 (CEN); Blake 2010 (CEN/TUR)
TX	Eagle Mtn SS	CEN	Emerson et al. 1994 (CEN); Akers & Akers 1997 (CEN); Cobban et al. 2008 (lowCEN); Scott 1977 (CEN)
TX	Edwards Lmst	ALB	Pittman 1959 (ALB); Clark 2009 (ALB); Allmon & Cohen 2008 (ALB); Macrostrat (ALB); Scott 1977 (ALB); Mancini & Puckett 2005 (mid/upALB in NW Gulf); COSUNA (ALB)
TX	El Picacho Fm	CAM/MAA	Emerson et al. 1994; Akers & Akers 1997; Lehman 1989a,b (MAA); Lehman 1985 (upMAA, equiv to Javelina Fm); Wagner 2001 (MAA Sierra Vieja Region = Javelina Fm in Big Bend Region); Lehman 2010 (MAA, corr w/ Javelina Fm in Brewster Co); NONMARINE
TX	Escondido Fm	MAA	Barrier 1980; Emerson et al. 1994; Akers & Akers 1997; Swezey & Sullivan 2004; Elder 1996; Snedden 1991 (MAA/DAN); Trevino et al. 2007 (upMAA); Stephenson & Reeside 1938 (MAA); Macrostrat (MAA/DAN); Hency 1987 (MAA); Elder 1996 (upMAA); COSUNA (MAA)

TX	Fredericksburg Grp	ALB	Kues 1989 (mid/upALB); Tappan 1943 (ALB); Emerson et al. 1994 (ALB); Akers & Akers 1997 (ALB); Clark 2009 (ALB); Allmon & Cohen 2008 (ALB); Macrostrat (ALB/CEN); Scott 1977 (ALB); Mancini & Puckett 2005 (midALB in NE Gulf)
TX	Comanche Peak (Fredericksburg Grp)	ALB	Kues 1989 (ALB Fredericksburg); Tappan 1943 (ALB); Emerson et al. 1994 (ALB); Akers & Akers 1997 (ALB); Clark 2009 (ALB); Allmon & Cohen 2008 (midALB); Macrostrat (ALB); Scott 1977 (ALB); Mancini & Puckett 2005 (midALB Fredericksburg Grp in NE Gulf); COSUNA (ALB)
TX	Goodland Lmst (Fredericksburg Grp)	ALB	Kues 1989 (ALB); Tappan 1943 (ALB); Emerson et al. 1994 (mid/upALB); Akers & Akers 1997 (ALB); Clark 2009 (ALB Fredericksburg); Allmon & Cohen 2008 (ALB Fredericksburg); Macrostrat (ALB); Scott 1977 (ALB); Mancini & Puckett 2005 (midALB Fredericksburg Grp in NE Gulf); COSUNA (ALB)
TX	Walnut Clay (Fredericksburg Grp)	ALB	Kues 1989 (midALB); Tappan 1943 (ALB); Emerson et al. 1994 (ALB); Akers & Akers 1997 (ALB); Clark 2009 (ALB); Allmon & Cohen 2008 (ALB); Macrostrat (ALB); Scott 1977 (ALB); Mancini & Puckett 2005 (midALB in NW Gulf); COSUNA (ALB)
TX	Gober Chk	CAM	Alshuaibi 2006 (lowest CAM); Emerson et al. 1994 (CAM); Akers & Akers 1997 (CAM); Hazel & Paulson 1964 (CAM); Macrostrat (SAN/CAM "Fm"); Hancock 1993 (lowCAM); Hency 1987 (CAM); COSUNA (SAN/CAM "Tongue")
TX	Kemp Clay	MAA	Barrier 1980; Emerson et al. 1994; Akers & Akers 1997; Mancini et al. 2008 (upMAA for western Gulf Coast); Elder 1996; Young 1986 (upMAA); Stephenson & Reeside 1938; Clark 2009 (MAA); Macrostrat (MAA); Hency 1987 (MAA); Elder 1996 (upMAA); COSUNA (MAA)
TX	Kiamichi Fm	ALB	Kues 1989 (upALB); Tappan 1943 (ALB); Emerson et al. 1994 (ALB Fredericksburg Grp); Akers & Akers 1997 (ALB Fredericksburg Grp); Allmon & Cohen 2008 (ALB); Macrostrat (ALB/CEN as Washita Grp); Scott 1977 (ALB); COSUNA (ALB)
TX	Marlbrook Marl	CAM	Emerson et al. 1994 (CAM); Akers & Akers 1997 (CAM); Mancini et al. 2008 (upCAM for western Gulf Coast); Trevino et al. 2007 (lowMAA); Marks & Stam 1983 (CAM/MAA in SW AR); Clark 2009 (CAM); Macrostrat (CAM/MAA); Mancini & Puckett 2005 (CAM); Elder 1996 (midCAM); COSUNA (CAM/MAA)
TX	Nacatoch Sand	CAM (up)/MAA	Kennedy et al. 2000 (uppermost CAM in TX, lowermost MAA in AR); Mancini et al. 2008 (upCAM for western Gulf Coast); Barrier 1980 (MAA); Emerson et al. 1994 (CAM); Akers & Akers 1997 (CAM); Marks & Stam 1983 (MAA); Stephenson & Reeside 1938 (MAA); Macrostrat (MAA); Mancini & Puckett 2005 (upCAM in NW Gulf); Hency 1987 (MAA); COSUNA (MAA)

TX	Navarro Grp	CAM/MAA	Akers & Akers 1997 (CAM/MAA); Emerson et al. 1994 (CAM/MAA); Young 1986 (MAA); Stephenson & Reeside 1938 (MAA); Clark 2009 (MAA); Macrostrat (CAM-DAN); COSUNA (MAA); USGS DB (CAM/MAA)
TX	Neylandville Marl Navarro Grp	CAM/MAA	Emerson et al. 1994 (CAM); Akers & Akers 1997 (CAM); Clark 2009 (MAA); Macrostrat (MAA); Marks & Stam 1983 (MAA); Hency 1987 (MAA); COSUNA (MAA)
TX	Ojinaga Fm	CEN-CAM	Emerson et al. 1994; Akers & Akers 1997; Cobban et al. 2008 (CEN-SAN); Powell 1965 (CEN/CON); Lehman 1989b (upCEN-lowCAM); Lehman 1985; Wagner 2001 (CEN-CAM Sierra Vieja Region); Lehman 2010 (CEN-lowCAM); Waggoner 2006 (lowCAM)
TX	Olmos Fm	MAA	Barrier 1980 (MAA); Emerson et al. 1994 (MAA); Akers & Akers 1997 (MAA); Elder 1996 (CAM/MAA); Snedden 1991 (MAA); Estrada-Ruiz et al. 2010 (upCAM/lowMAA in Mexico); Trevino et al. 2007 (lowMAA); Marks & Stam 1983; Stephenson & Reeside 1938 (MAA); Macrostrat (CAM/MAA); Hency 1987 (MAA); Elder 1996 (upCAM/lowMAA); COSUNA (CAM/MAA)
TX	Pecan Gap Fm	CAM	Barrier 1980; Emerson et al. 1994; Akers & Akers 1997; Mancini et al. 2008 (midCAM for Wm Gulf Coast); Swezey & Sullivan 2004; Elder 1996; Trevino et al. 2007 (upCAM); Marks & Stam 1983; Young 1986 (midCAM); Hazel & Paulson 1964; Stephenson & Reeside 1938; Macrostrat (CAM); Hancock 1993 (midCAM); Hency 1987 (CAM); Chimene & Maddocks 1984 (CAM); Locke & Gartner 1994 (CAM); Elder 1996 (midCAM); COSUNA (CAM)
TX	Pen Fm	CON-CAM	Emerson et al. 1994 (CON/SAN); Akers & Akers 1997 (CON); Cobban et al. 2008 (CAM); Horton 2006 (SAN/CAM); Kennedy & Cobban 2001 (midCAM at least in part); Kennedy & Cobban 1991 (SAN middle Pen, extends to lowCAM); Erdlac Jr. 1990 (CON-CAM); Ashmore 2003 (SAN/CAM); Lehman 1985 (Pen + Boquillas spans CEN-lowCAM); Wagner 2001 (SAN/CAM in Big Bend region); Lehman 2010 (CEN-lowCAM in Brewster Co TX); Roberts et al. 2005 (midCAM); Macrostrat (CON/SAN); Waggoner 2006 (lowCAM = Terlingua Fm); Jinnah et al. 2009 (low/midCAM); COSUNA (CON/SAN)
TX	Roxton Lmst	CAM	Cobban & Kennedy 1992 (CAM Roxton Mbr of Gober Chk); all other ref's for Gober Chk = CAM, so if is a mbr, then is CAM
TX	San Carlos SS	CON-CAM	Emerson et al. 1994; Akers & Akers 1997; Cobban et al. 2008 (CAM); Lehman 1989b (CAM); Lehman 1985 (CAM, equiv to Aguja Fm in Tornillo Basin); Wagner 2001 (CAM Sierra Vieja Region); Lehman 2010 (CAM); Waggoner 2006 (lowCAM); PREDOMINATELY NONMARINE
TX	San Miguel Fm	CAM/MAA	Barrier 1980 (MAA); Emerson et al. 1994 (CAM); Akers & Akers 1997 (CAM); Snedden 1991 (MAA); Trevino et al. 2007 (lowMAA); Marks & Stam 1983 (MAA); Stephenson & Reeside 1938 (CAM); Macrostrat (CAM); Hency 1987 (CAM/MAA); Elder 1996 (mid/upCAM); COSUNA (CAM)

TX	Sprinkle Fm	CAM	Akers & Akers 1997 (CAM); Emerson et al. 1994 (CAM); Young 1986 (lowCAM); USGS DB (CAM); Hency 1987 (CAM); Chimene & Maddocks 1984 (CAM); Ross & Maddocks 1983 (CAM); Elder 1996 (low/midCAM)
TX	Taylor Grp	CAM	Barrier 1980 (CAM "Fm"); Emerson et al. 1994 (CAM/MAA); Akers & Akers 1997 (MAA); Young 1986 (mid/upCAM); Hazel & Paulson 1964 (CAM lower Taylor); Stephenson & Reeside 1938 (CAM); Clark 2009 (SAN/CAM); Macrostrat (CAM-DAN); USGS DB (CAM); Marks & Stam 1983 (CAM); Emerson et al. 1994 (CAM); Hency 1987 (CAM lower Taylor); Chimene & Maddocks 1984 (CAM); Ross & Maddocks 1983 (CAM); Locke & Gartner 1994 (CAM); COSUNA (CAM/MAA)
TX	Bergstrom Fm (Taylor Grp)	CAM	Akers & Akers 1997 (CAM); Emerson et al. 1994 (CAM); Young 1986 (upCAM); USGS DB (CAM); Hency 1987 (MAA); Chimene & Maddocks 1984 (CAM); Kennedy & Cobban 1999 (CAM)
TX	Terlingua Fm	CEN-CAM??	Ashmore 2003 (TUR-CAM); Akers & Akers 1997 (CEN-CON); Horton 2006 (Terlingua Crk SS Mbr/Aguja Fm = CAM); Lehman 1991 (upCAM Terlingua Crk SS Mbr/Aguja Fm); Rowe et al. 1992 (CAM); Emerson et al. 1994 (CEN-SAN); Wagner 2001 (CAM Terlingua SS Mbr/Aguja Fm); USGS DB (CEN-SAN); Hency 1987 (CEM-CAM); Waggoner 2006 (= Pen Fm which is lowCAM, Terlingua Crk SS/Aguja = CAM); COSUNA (CEN-SAN)
TX	Washita Grp	ALB/CEN	Kues 1989 (ALB/CEN); Tappan 1943 (ALB); Akers & Akers 1997 (ALB/CEN); Emerson et al. 1994 (ALB/CEN); Mancini et al. 2008 (lowCEN for western Gulf Coast); Huffman 1960 (lowCEN); Imlay 1945 (ALB/CEN); Young 1986 (upALB/lowCEN); Ambrose et al. 2009 (CEN); Allmon & Cohen 2008 (ALB/CEN); Kirkland et al. 1999 (ALB/CEN); Clark 2009 (up-mostALB/CEN); Macrostrat (ALB/CEN); Hopkins et al. 1999 (ALB/CEN); Scott 1977 (ALB/CEN); Mancini & Puckett 2005 (upALB/lowCEN in NE Gulf); COSUNA (ALB/CEN)
TX	Denton Fm Washita Grp)	ALB	Kues 1989 (ALB); Tappan 1943 (ALB); Emerson et al. 1994 (ALB); Akers & Akers 1997 (ALB); Allmon & Cohen 2008 (upALB); Macrostrat (ALB); Hopkins et al. 1999 (upALB); Scott 1977 (ALB); Mancini & Puckett 2005 (upALB/lowCEN Washita Grp in NE Gulf); COSUNA (ALB)
TX	Duck Crk Fm (Washita Grp)	ALB	Kues 1989 (ALB); Emerson et al. 1994 (ALB); Akers & Akers 1997 (ALB); Allmon & Cohen 2008 (upALB); Macrostrat (ALB/CEN); Hopkins et al. 1999 (upALB); Scott 1977 (ALB); Mancini & Puckett 2005 (upALB/lowCEN Washita Grp in NE Gulf); COSUNA (ALB)
TX	Fort Worth Lmst (Washita Grp)	ALB	Emerson et al. 1994 (ALB); Akers & Akers 1997 (ALB); Allmon & Cohen 2008 (upALB); Macrostrat (ALB); Hopkins et al. 1999 (upCEN); Scott 1977 (ALB); Mancini & Puckett 2005 (upALB/lowCEN Washita Grp in NE Gulf); COSUNA (ALB)

TX	Grayson Marl (Washita Grp)	CEN	Kues 1989 (lowCEN); Barrier 1980 (ALB/CEN); Emerson et al. 1994 (ALB/CEN); Akers & Akers 1997 (CEN); Imlay 1945 (CEN); Ambrose et al. 2009 (CEN); Allmon & Cohen 2008 (lowCEN); Tappan 1943 (ALB); Clark 2009 (CEN); Macrostrat DB (CEN); Hopkins et al. 1999 (CEN); Scott 1977 (CEN); Mancini & Puckett 2005 (lowCEN in NW Gulf); Hancey 1987 (CEN); COSUNA (CEN)
TX	Georgetown Lmst (Washita Grp)	ALB/CEN	Emerson et al. 1994 (ALB/CEN); Mancini et al. 2008 (lowCEN Georgetown for Wm Gulf Coast); Akers & Akers 1997 (ALB/CEN); Clark 2009 (ALB/CEN); Getzandner 1930 (ALB/CEN); Imlay 1945 (ALB); Young 1986 (ALB/CEN); Ambrose et al. 2009 (ALB/CEN); Allmon & Cohen 2008 (ALB/CEN); Macrostrat (ALB/CEN); Scott 1977 (ALB/CEN); Mancini & Puckett 2005 (upALB in NW Gulf); COSUNA (ALB/CEN)
TX	Main Street Lmst (Washita Grp)	ALB/CEN	Kues 1989 (lowCEN); Emerson et al. 1994 (ALB/CEN); Akers & Akers 1997 (CEN/ALB); Imlay 1945 (ALB); Allmon & Cohen 2008 (lowCEN); Tappan 1943 (ALB); Siverson et al. 2007 (upALB); Macrostrat DB (ALB/CEN); Hopkins et al. 1999 (CEN); Scott 1977 (CEN); COSUNA (CEN)
TX	Pawpaw (Washita Grp (Denison))	ALB	Kues 1989 (ALB/lowCEN); Tappan 1943 (ALB); Emerson et al. 1994 (ALB); Akers & Akers 1997 (ALB); Spangler & Peterson 1950 (ALB); Allmon & Cohen 2008 (ALB/CEN); Siverson et al. 2007 (upALB); Hopkins et al. 1999 (ALB/CEN); Scott 1977 (ALB); Mancini & Puckett 2005 (upALB/lowCEN Washita Grp in NE Gulf); COSUNA (ALB)
TX	Weno Fm	ALB	Allmon & Cohen 2008 (ALB); Siverson et al. 2007 (upALB); Beikirch & Feldmann 1980 (ALB); Hopkins et al. 1999 (upALB); Scott 1977 (ALB); Allmon 2004 (ALB); COSUNA (ALB)
TX	Woodbine Fm	CEN/TUR	Barrier 1980 (CEN); Emerson et al. 1994 (CEN); Mancini et al. 2008 (upCEN in western Gulf Coast); Akers & Akers 1997 (CEN); Myers 2010 (CEN); Huffman 1960 (CEN); Ambrose et al. 2009 (CEN); Allmon & Cohen 2008 (CEN); Stephenson & Reeside 1938 (CEN); Kirkland et al. 1999 (CEN); Macrostrat (CEN/TUR); Mancini & Puckett 2005 (mid/upCEN in NW Gulf); Dawson 1997 (CEN in part); Liro et al. 1994 (CEN); Brown & Pierce 1962 (CEN); Dawson 2000 (CEN); Christopher 1982 (CEN in part); COSUNA (CEN); Hancock 2004 (low/midCEN)
TX	Wolfe City Fm	CAM	Barrier 1980 (CAM); Emerson et al. 1994 (CAM); Akers & Akers 1997 (CAM); Mancini et al. 2008 (midCAM for Wm Gulf Coast); Cobban & Kennedy 1993 (midCAM); Marks & Stam 1983 (CAM); Hazel & Paulson 1964 (CAM); Stephenson & Reeside 1938 (CAM); Clark 2009 (CAM); Macrostrat (CAM); Mancini & Puckett 2005 (midCAM); Hancey 1987 (CAM); Locke & Gartner 1994 (CAM); COSUNA (CAM)

UT	Blair Fm	CAM	Finn 2005 (CAM in WY); Loseth et al. 2006 (lowCAM); Finn & Johnson 2005 (CAM); Macrostrat (TUR); Jinnah et al. 2009 (lowCAM)
UT	Burro Canyon Fm	APT-CEN	Simmons 1957 (correlates w/ Cedar Mtn Fm in UT = ALB/CEN); Miller 1987 (correlates w/ Cedar Mtn Fm in UT = ALB/CEN); Aubrey 1989 (ALB/APT); Kirkland et al. 1999 (equiv to Ruby Ranch Mbr/Cedar Mtn Fm = APT/ALB); Eaton & Cifelli 2001 (ALB/CEN); USGS DB (BARR-ALB); DeCelles & Coogan 2006 (HAUT-ALB); Macrostrat (HAUT-ALB); NONMARINE in CO
UT	Castlegate SS	CAM	Lawton et al. 2003 (midCAM); Robinson 2005 (mid/upCAM); Maiall & Arush 2001 (CAM); Robinson & Slingerland 1998 (CAM); Miall 1993 (CAM); McLaurin & Steel 2000 (midCAM); Gallin et al. 2010 (CAM); Aschoff & Steel 2011 (mid/upCAM); Jinnah et al. 2009 (mid/upCAM); Johnson 1987 (CAM); Krystinik & DeJarnett 1995 (mid/upCAM)
UT	Cedar Mtn Fm	ALB/CEN	Cifelli 1999 (ALB/CEN); Aubrey 1989 (ALB); Young 1960 (ALB/CEN); Ryer 1983 (ALB/CEN); Kirkland et al. 1999 (BARR-CEN); Eaton & Cifelli 2001 (ALB/CEN); Nydam & Cifelli 2002 (ALB/CEN); USGS DB (ALB/CEN); DeCelles & Coogan 2006 (HAUT-ALB); Macrostrat (APT/ALB); COSUNA (APT/ALB); NONMARINE
UT	Dakota SS	ALB/CEN	Heaton 1950 (CEN); Aubrey 1989 (CEN); Johnson 2003 (CEN); Cobban & Reeside 1952a (CEN); Edwards et al. 2005 (CEN); Ryer 1983 (ALB/CEN); Kirkland et al. 1999 (CEN); USGS DB (ALB/CEN); Kirschbaum & Roberts 2005 (CEN); Eaton 1991 (CEN); Eaton et al. 1999 (CEN); Macrostrat (ALB/CEN in NM, APT-TUR "Fm/Grp", BERR-TUR for "Grp"); COSUNA (ALB/CEN); Edwards et al. 2005 (CEN); Goldstrand 1994 (CEN); Tibert et al. 2009 (CEN); Leithold 1994 (into upCEN); Cobban et al. 2000 (CEN/TUR); Sethi & Leithold 1997 (into upCEN); Sageman 1996 (CEN); lower 1/2 Dakota is NONMARINE
UT	Echo Canyon Conglomerate	CON-MAA	Lehman 1987 (MAA, correlates w/ Price River = CAM/MAA); Kilbourne 1969 (correlates w/ Ericson SS/Mesaverde in WY = CAM/MAA); USGS DB (CON-SAN); Wiltchko & Dorr 1983 (CON); DeCelles 1994 (CON/SAN); DeCelles & Cavazza 1999 (SAN); Macrostrat (CAM); COSUNA (CAM); NONMARINE
UT	Frontier Fm	CEN-CON	Johnson 2003 (TUR); Cobban & Reeside 1952a,b (TUR); Young 1960 (TUR); USGS DB (ALB-CON); Bhattacharya & Willis 2001 (CEN/TUR in WY); Willis et al. 1999 (CEN/TUR in WY); Ryer 1977 (ALB-CON); Finn 2005 (CEN-CON); DeCelles & Cavazza 1999 (CEN/TUR); Kirschbaum & Roberts 2005 (CEN/TUR); Macrostrat (TUR "SS" or ALB-SAN "Fm"); COSUNA (CEN-SAN); Nichols & Sweet 1993 (CEN/TUR in WY); Wiltchko & Dorr 1983 (TUR/CON); Nichols & Jacobson 1982 (CEN/TUR Frontier); Finn & Johnson 2005 (CEN-CON)

UT	Henefer Fm	TUR-CAM	Cobban & Reeside 1952a (CON/SAN); Cobban & Reeside 1952b (CON/SAN+); USGS DB (Paleocene); DeCelles 1994 (TUR/CON); DeCelles & Cavazza 1999 (TUR/CON); Macrostrat (SAN/CAM); COSUNA (SAN); at least partially NONMARINE
UT	Hilliard Sh	CON/SAN	Heaton 1950 (MAA in WY); Nichols & Sweet 1993 (CON/SAN in WY); USGS DB (CON/SAN); Witschko & Dorr 1983 (TUR-SAN); DeCelles 1994 (SAN); Finn 2005 (CON/SAN); Kirschbaum & Roberts 2005 (TUR/CON); Finn & Johnson 2005 (CON/SAN); COSUNA (CON)
UT	Indianola Grp	ALB-CAM	Stephenson & Reeside 1938 (CEN-SAN); Cobban & Reeside 1952a (CEN-SAN); Horton et al. 2004 (ALB-CAM); Maill & Arush 2001 (into CAM); Robinson & Slingerland 1998 (TUR-CAM at least); USGS DB (CEN-CAM); Dickinson et al. 1986 (SAN/CAM at least); DeCelles & Coogan 2006 (ALB-CAM); Lawton 1985 (ALB-CAM); Talling et al. 1995 (SAN/CAM at least); Macrostrat (BERR-SAN); COSUNA (CON/SAN); PREDOMINATELY NONMARINE
UT	Iron Springs Fm	CEN/TUR	Cobban & Reeside 1952a (CEN/TUR); Eaton 1999 (CEN-SAN); Goldstrand 1994 (CEN-CAM); Tibert et al. 2009 (TUR-CON); USGS DB (CEN/TUR); Macrostrat (CEN-MAA); COSUNA (CEN-MAA); Ryer 1983 (CEN/TUR) NONMARINE
UT	Kaiparowits Fm	CAM/MAA	Heaton 1950 (DAN); Cobban & Reeside 1952a (MAA); Miall 1993 (CAM/MAA); Robinson 2005 (CAM at least); Yoshida 2000 (CAM/MAA); Eaton 1999 (CAM at least); Goldstrand 1994 (CAM); Tibert et al. 2009 (CAM); USGS DB (CAM); Cifelli 1990 (CAM); Roberts et al. 2005 (CAM); Eaton et al. 1999 (CAM); Gates & Sampson 2007 (upCAM); Macrostrat (SAN-MAA); Gallin et al. 2010 (CAM); Jinnah et al. 2009 (upCAM); COSUNA (MAA); NONMARINE
UT	Mancos Sh	CEN-CAM	Heaton 1950 (CEN-SAN); Kirkland et al. 1999 (starts CEN/TUR); Aubrey 1989 (starts CEN); Hettinger & Kirschbaum 2002 (CEN-CAM); Johnson 2003 (CEN-CAM); Shanley & McCabe 1995 (into SAN); Cobban & Reeside 1952a,b (ALB-CAM); Young 1960 (starts TUR); Birkhead 2005 (into midCAM); Edwards et al. 2005 (into upSAN); Hettinger & Kirschbaum 2002 (CEN-CAM); Johnson et al. 2005 (into CAM); Pattison 1995 (into CAM); Robinson & Slingerland 1998 (TUR-CAM at least); Robinson 2005 (into CAM); Ryer 1983 (CEN-CAM); Taylor et al. 2002 (into CAM); Kirkland et al. 1999 (CEN start); USGS DB (ALB-CAM); Roberts et al. 2005 (into CAM); Macrostrat (CEN-CAM); COSUNA (CEN-CAM)

UT	Anchor Mine Tongue (Mancos Sh)	CAM	Birkhead 2005 (<i>Baculites scottii</i> zone = midCAM); Robinson 2005 (underlies Sego SS = CAM); Willis & Gabel 2001 (equiv to late Sego SS = upCAM); Willis & Gabel 2003 (btwn lower & upper Sego SS = CAM); Klein et al. 1999 (above Castlegate = CAM); York et al. 2011 (splits Sego = midCAM); Warner 1964 (btwn parts of Sego = midCAM); Aschoff & Steel 2011 (midCAM); Krystinik & DeJarnett 1995 (midCAM)
UT	Blackhawk Fm (Mancos Sh)	CAM	Edwards et al. 2005 (CAM); USGS DB (CAM); Adams & Bhattacharya 2005 (CAM); Birkhead 2005 (CAM); Dickinson et al. 1986 (CAM); Horton et al. 2004 (CAM); Johnson et al. 2005 (CAM); Lawton 1985 (CAM); Miall & Arush 2001 (CAM); Miall 1993 (CAM); Pattison 1995 (CAM); Robinson & Slingerland 1998 (CAM); Robinson 2005 (CAM); Yoshida 2000 (midCAM); Heaton 1950 (CAM); McLaurin & Steel 2000 (lowCAM); Lawton et al. 2003 (CAM); Gallin et al. 2010 (CAM); Jinnah et al. 2009 (lowCAM); Krystinik & DeJarnett 1995 (low/midCAM)
UT	Blue Gate Mbr (Mancos Sh)	CON/SAN	Johnson 2003 (CON-CAM); Edwards et al. 2005 (CON-CAM); USGS DB (upTUR-CAM); Condon 2003 (CON/SAN); Fielding 2010 (upCON/SAN); Gardner 1995 (CON in part); Lawton 1985 (CON/SAN); Robinson & Slingerland 1998 (CON/SAN); Ryer 1991 (CON/SAN); Lawton et al. 2003 (CON/SAN); Gallin et al. 2010 (CON/SAN); Martinson et al. 1998 (CON-CAM)
UT	Emery SS (Mancos Sh)	SAN	Edwards et al. 2005 (SAN); USGS DB (SAN/CAM); Elder & Kirkland 1993 (SAN); Condon 2003 (SAN); Lawton 1985 (SAN); Pattison 1995 (SAN); Robinson & Slingerland 1998 (~SAN, nr CON boundary); Heaton 1950 (CON/SAN); Lawton et al. 2003 (SAN); Gallin et al. 2010 (SAN); Johnson 1987 (SAN/lowestCAM); Martinson et al. 1998 (SAN); Krystinik & DeJarnett 1995 (SAN)
UT	Ferron SS (Mancos Sh)	TUR	Edwards et al. 2005 (TUR); USGS DB (midTUR); Becker et al. 2010 (midTUR); Bhattacharya & Davies 2001 (upTUR); Ryer 1981 (upTUR); Bhattacharya & MacEachern 2009 (TUR); Condon 2003 (TUR); Fielding 2010 (mid/upTUR); Gardner 1995 (90.25 +/- 0.45Ma = midTUR); Lawton 1985 (TUR); Leithold 1993 (midTUR to start); Leithold 1994 (midTUR to start); Moiola et al. 2004 (TUR); Ryer 1981 (TUR); Ryer 1991 (TUR/CON); Sethi & Leithold 1997 (TUR in part); Lawton et al. 2003 (TUR); Gallin et al. 2010 (TUR/CON); Martinson et al. 1998 (TUR/low-mostCON)
UT	Garley Canyon Mbr (Mancos Sh)	SAN	USGS DB (SAN)
UT	Juana Lopez Mbr (Mancos Sh)		Edwards et al. 2005 (upTUR); in other states is TUR

UT	Star Point SS (Mancos Sh)	CAM	Edwards et al. 2005 (CAM); USGS DB (SAN/CAM); Adams & Bhattacharya 2005 (CAM); Birkhead 2005 (CAM); Condon 2003 (SAN in part); Johnson et al. 2005 (CAM); Lawton 1985 (CAM); Pattison 1995 (SAN/lowCAM); Robinson & Slingerland 1998 (CAM); Heaton 1950 (CAM); McLaurin & Steel 2000 (lowCAM in part); Lawton et al. 2003 (CAM); Gallin et al. 2010 (CAM); Martinson et al. 1998 (CAM in part); Krystinik & DeJarnett 1995 (SAN/CAM, Panther Tongue = lowCAM)
UT	Mesaverde Grp	CAM	Hettinger & Kirschbaum 2002 (CAM/MAA); Cobban & Reeside 1952a (CON-MAA); Cobban & Reeside 1952b (CON/SAN+); Johnson et al. 2005 (CAM); Miall 1993 (CAM/MAA); Robinson 2005 (at least CAM); Taylor et al. 2002 (CAM Castlegate Mbr at least); Yoshida 2000 (CAM/MAA); USGS DB (SAN/CAM); Finn 2005 (CAM in WY); Loseth et al. 2006 (at least CAM); Roberts et al. 2005 (at least CAM); Krystinik & DeJarnett 1995 (CAM/MAA); Macrostrat (TUR-MAA); COSUNA (TUR-MAA)
UT	Tununk Sh (Manco Sh) (Mesaverde Grp)	TUR	Leithold 1994 (latestCEN-midTUR); Gardner 1995 (TUR); Ryer 1983 (up-mostCEN?/TUR); Ryer 1981 (underlies Ferron SS = upTUR); Leithold 1993 (TUR); Sethi & Leithold 1994 (TUR); Cobban et al. 2000 (TUR); Bhattacharya & Davies 2001 (underlies Ferron SS = upTUR); Sethi et al. 1998 (upCEN/midTUR); Condon 2003 (TUR); Ryer 1991 (low/midTUR); Fielding 2010 (up-mostCEN/mostlyTUR); Bhattacharya & MacEachern 2009 (equiv to Ferron SS = TUR); Currie 2002 (TUR); Edwards et al. 2005 (midTUR); Sethi & Leithold 1997 (mid/upTUR); USGS DB (upCEN/midTUR); Ryer 1993 (CEN/TUR); Shanley & McCabe 1995 (TUR); Edwards et al. 2005 (TUR); Heaton 1950 (CON); Lawton et al. 2003 (up-mostCEN/TUR); Gallin et al. 2010 (upCEN/TUR); COSUNA (TUR-MAA Mesaverde Grp)
UT	Price River Fm	SAN-MAA	Cobban & Reeside 1952a (CAM/MAA); Hettinger & Kirschbaum 2002 (CAM, corr w/ Williams Fork = CAM/MAA in CO); Johnson 2003 (CAM/MAA); Stephenson & Reeside 1938 (MAA); Hettinger & Kirschbaum 2002 (CAM); Maiall & Arush 2001 (CAM); Horton et al. 2004 (CAM); Robinson & Slingerland 1998 (CAM); Pattison 1995 (at least CAM); Robinson 2005 (CAM); USGS DB (CAM); Talling et al. 1995 (CAM/MAA); Roberts et al. 2005 (upCAM); Macrostrat (CON-CAM); Adams & Bhattacharya 2005 (CAM); Horton et al. 2004 (CAM); COSUNA (CON-CAM); NONMARINE
UT	South Flat Fm	SAN-MAA	Maiall & Arush 2001 (CAM); Robinson & Slingerland 1998 (SAN/CAM); Robinson 2005 (CAM at least); USGS DB (SAN/CAM); Talling et al. 1995 (SAN/CAM); Hunt 1954 (CAM/MAA South Flat - btwn Indianola & Price River); Horton et al. 2004 (CAM); NONMARINE

UT	Straight Cliffs Fm	TUR-CAM	Allen & Johnson 2010a,b (TUR-CAM); USGS DB (midTUR-lowCAM); Macrostrat (CEN-CON); Eaton 1999 (TUR-SAN); Goldstrand 1994 (TUR-CAM); Leithold 1993 (midTUR to start); Leithold 1994 (midTUR to start); Ryer 1983 (TUR-SAN at least); Sethi & Leithold 1994 (midTUR to start); Sethi & Leithold 1997 (midTUR to start); Tibert et al. 2009 (CON/SAN); Heaton 1950 (CAM); Shanley & McCabe 1991 (TUR-CAM); Jinnah & Roberts 2011 (SAN/lowCAM in part); Castle et al. 2004 (TUR-CAM); Lawton et al. 2003 (TUR-SAN); Eaton 2006 (TUR-CAM); Hettlinger 2000 (TUR-CAM); Cobban et al. 2000 (midTUR-SAN in part); Gallin et al. 2010 (TUR-CAM); Jinnah et al. 2009 (CON-lowCAM in part); Foster et al. 2001 (midTUR-lowCAM); Sageman 1996 (midTUR at least to start)
UT	Drip Tank Mbr (Straight Cliffs Fm)	CAM	Allen & Johnson 2010a,b (CAM); USGS DB (lowCAM); Eaton 1999 (SAN); Shanley & McCabe 1991 (CAM); Jinnah & Roberts 2011 (lowCAM); Castle et al. 2004 (CAM); Lawton et al. 2003 (SAN); Eaton 2006 (lowCAM); Hettlinger 2000 (CAM); Gallin et al. 2010 (CAM); Jinnah et al. 2009 (lowCAM); Shanley & McCabe 1995 (lowCAM); NONMARINE
UT	John Henry Mbr (Straight Cliffs Fm)	CON/SAN	Allen & Johnson 2010a,b (CON/SAN); USGS DB (midCON-lowCAM); Becker et al. 2010 (CON/SAN); Eaton 1999 (CON/SAN); Edwards et al. 2005 (equiv to Emery SS = SAN); Ryer 1983 (CON/SAN); Shanley & McCabe 1991 (CON-CAM); Jinnah & Roberts 2011 (SAN in part); Castle et al. 2004 (CON/SAN); Lawton et al. 2003 (CON/SAN); Eaton 2006 (CON/SAN); Hettlinger 2000 (CON/SAN); Cobban et al. 2000 (upCON/SAN); Gallin et al. 2010 (CON/SAN); Jinnah et al. 2009 (CON/SAN); Shanley & McCabe 1995 (SAN)
UT	Smoky Hollow Mbr (Straight Cliffs Fm)	TUR/CON	Allen & Johnson 2010a,b (TUR/lowestCON); USGS DB (mid/upTUR); Becker et al. 2010 (TUR); Eaton & Ciffeli 2001 (TUR); Eaton 1999 (TUR); Ryer 1983 (TUR/lowestCON, boundary is ambiguous); Shanley & McCabe 1991 (TUR/lowestCON); Castle et al. 2004 (TUR/lowestCON); Lawton et al. 2003 (TUR/lowestCON); Eaton 2006 (TUR); Hettlinger 2000 (TUR/CON); Cobban et al. 2000 (upTUR/midCON); Gallin et al. 2010 (CON); Jinnah et al. 2009 (TUR); Shanley & McCabe 1995 (upTUR); NONMARINE
UT	Tibbet Canyon Mbr (Straight Cliffs Fm)	TUR	Allen & Johnson 2010a,b (TUR); USGS DB (midTUR); Becker et al. 2010 (TUR); Eaton 1999 (TUR); Ryer 1983 (TUR/CON, boundary is ambiguous); Ryer 1993 (midTUR); Shanley & McCabe 1991 (TUR); Castle et al. 2004 (TUR); Lawton et al. 2003 (TUR); Eaton 2006 (TUR); Hettlinger 2000 (TUR); Cobban et al. 2000 (mid/upTUR); Gallin et al. 2010 (TUR); Shanley & McCabe 1995 (upTUR)

UT	Tropic Sh	CEN/TUR	Heaton 1950 (CAM); Shanley & McCabe 1995 (midTUR); Cobban & Reeside 1952a (CEN/TUR); Allen & Johnson 2010 (TUR); Ryer 1983 (TUR); Eaton 1991 (up-mostCEN/TUR); Goldstrand 1994 (CEN/TUR); Tibert et al. 2009 (CEN/TUR); USGS DB (CEN/TUR); Eaton et al. 1999 (CEN/TUR); Macrostrat (CEN); Leithold 1994 (up-mostCEN/midTUR); Cobban et al. 2000 (CEN/TUR); Sethi & Leithold 1997 (up-mostCEN/midTUR); Ryer 1993 (CEN/TUR); Sageman 1996 (CEN/TUR)
WY	Adaville Fm	SAN/CAM	Heaton 1950 (DAN); Nichols & Sweet 1993 (SAN/CAM corr w/ Telegraph Crk in MT); Wiltshcko & Dorr 1983 (CAM); Nichols & Jacobson 1982 (starts lowCAM); Miller 1977 (CAM); Liu et al. 2005 (CAM); Johnson et al. 2005 (SAN/CAM); Lawrence 1992 (SAN/CAM); Macrostrat (TUR); Krystinik & DeJarnett 1995 (lowCAM); COSUNA (TUR); NONMARINE
WY	Bacon Ridge SS	CON-CAM	Wiltshcko & Dorr 1983 (CON Bacon Ridge SS "equivalent"); Hicks et al. 1999 (SAN/CAM); Harris et al. 1996 (CON); Schmitt & Steidtmann 1990 (SAN); Hicks et al. 1995 (SAN/CAM); Leier 2000 (CON/SAN); Macrostrat (CEN/TUR); COSUNA (CEN/TUR)
WY	Baxter Sh	TUR-CAM	Wiltshcko & Dorr 1983 (CON/SAN); Finn 2005 (CON/SAN); Loseth et al. 2006 (lowCAM); Kirschbaum & Roberts 2005 (CON start); Finn & Johnson 2005 (CON/SAN); Mederos et al. 2005 (TUR-SAN); Miller 1977 (at least CAM); Liu & Nummedal 2004 (top-mostTUR-SAN); Martinsen et al. 1999 (at least into SAN/lowestCAM); Johnson et al. 2005 (TUR-CAM); Macrostrat (CEN/TUR); Jinnah et al. 2009 (CON-CAM in part); Martinsen 2003 (CON-CAM); Uroza 2008 (lowCAM at least in part); Krystinik & DeJarnett 1995 (lowCAM); COSUNA (CEN/TUR)
WY	Bearpaw Sh	CAM/MAA	Stephenson & Reeside 1938 (MAA in MT); Tibert et al. 2009 (CAM/MAA in northern Plains); Swift et al. 1985 (MAA in central rockies); Hicks et al. 1999 (MAA); USGS DB (upCAM/lowMAA); Hicks et al. 1995 (CAM/MAA); Finn 2010 (MAA); Macrostrat (CAM/MAA); Martinsen 2003 (CAM/MAA); Bergstresser & Krebs 1983 (upCAM/MAA)
WY	Belle Fourche Sh	CEN	Kirkland et al. 1999 (CEN); Tibert et al. 2009 (CEN in northern Plains); Nichols & Jacobson 1982 (CEN); Kirschbaum & Roberts 2005 (CEN); Oboh-Ikuenobe et al. 2007 (CEN); Ryer 1993 (lowestCEN/midTUR); Yang & Miall 2009 (CEN in northern Great Plains); Bhattacharya & Willis 2001 (CEN/TUR); Willis et al. 1999 (CEN/TUR); Winn 1989 (CEN/TUR); Liu et al. 2005 (CEN); USGS DB (CEN); Eicher 1967 (CEN); Macrostrat (CEN "Sh" or ALB/CEN "Fm"); Cobban & Larson 1997 (low/midCEN); Cobban et al. 1959 (CEN); Martinsen 2003 (CEN); COSUNA (ALB/CEN)

WY	Blind Bull Fm	CON/SAN	Wiltshko & Dorr 1983 (correlates w/ Frontier = CEN-CON & Hilliard = CON/SAN in WY); Nichols & Jacobson 1982 (correlates w/ Hilliard which in UT = CON/SAN); Macrostrat (ALB-TUR); COSUNA (ALB-TUR)
WY	Carlile Sh	TUR	Kirkland et al. 1999 (TUR); Heaton 1950 (CON); Stephenson & Reeside 1938 (TUR in Great Plains); Tibert et al. 2009 (TUR in northern Plains); Nichols & Jacobson 1982 (TUR); Merewether et al. 2007 (TUR); Yang & Miall 2009 (TUR in northern Great Plains); Lui & Nummedal 2004 (TUR); Winn 1989 (TUR/CON); Liu et al. 2005 (TUR); USGS DB (TUR-SAN); Cobban 1984 (TUR); Macrostrat (TUR or CEN-CON); Cobban & Larson 1997 (mid/upTUR); Cobban et al. 1959 (TUR); Martinsen 2003 (CON); COSUNA (CEN/TUR)
WY	Sage Breaks Sh Mbr (Carlile Sh)	TUR-SAN	USGS DB (TUR); Nichols & Jacobson 1982 (TUR/CON); Cobban & Reeside 1952b (TUR in Great Plains composite sxn, TUR possibly into CON in WY); Tillman & Almon 1979 (TUR); Winn 1989 (CON); Martinson et al. 1998 (CON/SAN); Frerichs 1980 (equiv to lower Kevin Mbr = CON/SAN); Merewether & Claypool 1980 (CON/SAN); Frerichs 1979 (CON-CAM); Serbeck 1981 (CON-CAM)
WY	Cody Sh	CON-CAM	Heaton 1950 (SAN); Tibert et al. 2009 (CON in N-Plains); Wiltshko & Dorr 1983 (CON Cody Sh "equivalent"); Kirschbaum & Roberts 2005 (starts CON); Merewether et al. 2007 (TUR/CON start); Miller 1977 (into CAM); Hicks et al. 1999 (into SAN); Willis et al. 1999 (SAN/CAM); Winn 1989 (TUR/CON at least); Harris et al. 1996 (CON); Schmitt & Steidtmann 1990 (CON); Macrostrat (CEN-SAN); USGS DB (CEN-CAM); Schultz et al. 1976 (<i>Baculites perplexus</i> zone & correlates w/ Claggett SS = midCAM); Nichols & Sweet 1993 (CEN-SAN in MT); Tysdal & Nichols 1991 (CON/SAN); Bergman 1994 (into lowCAM); Hicks et al. 1995 (into SAN); Finn 2010 (CON-CAM); Jinnah et al. 2009 (CON-lowCAM); Martinsen 2003 (CON-CAM); COSUNA (CEN-CON); Nichols & Jacobson 1982 (CEN-SAN Cody in MT); Kirschbaum & Roberts 2005 (starts CON); Cobban & Reeside 1952b (CEN-SAN in part)
WY	Steele Sh Mbr (Cody Sh)	TUR-CAM	USGS DB (CAM); Macrostrat (CEN-CON); Finn & Johnson 2005a,b (TUR-CAM); Finn 2005 (TUR-CAM); Johnson et al. 2005a (TUR-CAM); Johnson et al. 2005b (CON-CAM); Cobban 1962 (<i>Baculites perplexus</i> zone in uppermost Steele Sh = midCAM); Dymann & Condon 2007 (CAM); Liu et al. 2005 (CAM); Painter 2009 (CAM); Martinsen 2003 (CON-CAM); Brenner 1978 (CAM); Mellere 1996 (into CAM); Martinson et al. 1998 (CAM at least in part); Uroza 2008 (CAM at least in part); Brain 1993 (low/midCAM); Krystinik & DeJarnett 1995 (CAM); COSUNA (CEN-CON)
WY	Cow Crk SS Mbr (Steele Sh) (Cody Sh)	CAM	USGS DB (CAM); Mellere 1996 (lowCAM); Mellere & Steel 1995 (midCAM)

WY	Fishtooth SS (Steele Sh) (Cody Sh)	CAM	USGS DB (lowCAM); Finn & Johnson 2005 (CAM); Johnson et al. 2005a,b (CAM); Krystinik & DeJarnett 1995 (lowCAM)
WY	Shannon SS Mbr (Steele Sh) (Cody Sh)	CAM	USGS DB (CAM); Finn & Johnson 2005 (CAM); Johnson et al. 2005a,b (CAM); Dyman & Condon 2007 (upper Steele sh and equiv to Haystack Mtns Fm = CAM); Bergman 1994 (lowCAM); Walker & Bergman 1993 (lowCAM); Bergman & Walker 1995 (lowCAM); Painter 2009 (81Ma = lowCAM); Martinsen 2003 (lowCAM); Brenner 1978 (CAM); Gani & Bhattacharya 2007 (SAN); Gani et al. 2008 (SAN); Krystinik & DeJarnett 1995 (lowCAM)
WY	Sussex SS Mbr (Steele Sh) (Cody Sh)	CAM	USGS DB (CAM); Finn & Johnson 2005 (CAM); Johnson et al. 2005a,b (CAM); Cobban 1962 (<i>Bactulites obtusus</i> zone = midCAM just below Sussex Mbr); Asquith 1970 (lowCAM, as mbr of Pierre Sh); Martinsen 2003 (lowCAM); Brenner 1978 (CAM); Krystinik & DeJarnett 1995 (lowCAM)
WY	Eagle SS	SAN/CAM	Heaton 1950 (SAN); Nichols & Jacobson 1982 (CAM); Roberts et al. 2005 (CAM in MT); Hicks et al. 1999 (CAM); USGS DB (SAN/CAM); Asquith 1970 (CAM); Nichols & Sweet 1993 (CAM); Tysdal & Nichols 1991 (upSAN); Shelton 1965 (CAM in MT); Hicks et al. 1995 (CAM); Payenberg et al. 2002 (SAN/CAM in MT); Payenberg et al. 2003 (SAN/CAM); Robinson et al. 1959 (CAM in MT); He et al. 2005 (CAM); Finn 2010 (CAM in MT); Macrostrat (TUR-CAM); Bertog et al. 2007 (lowCAM in MT); Bertog 2002 (into lowCAM in MT); Jinnah et al. 2009 (lowCAM); COSUNA (TUR)
WY	Elk Basin SS	CAM	Cobban & Kennedy 1992 (as mbr of Telegraph Crk); Hicks et al. 1995 (lowCAM); Hicks et al. 1999 (lowCAM); McCabe 1948 (equiv to Telegraph Crk = SAN/CAM); Hammer & Lloyd 1925 (mbr of Telegraph Crk); Engelder et al. 1997 (CAM); Miller et al. 1965 (Elk Basin SS as well as Telegraph Crk & Virgille SS in the "Eagle SS interval"); Klug 1992 (<i>Scaphites hippocrepis</i> I zone = lowCAM)
WY	Everts Fm	SAN/CAM	Roberts et al. 2005 (CAM in MT); Tysdal & Nichols 1991 (upSAN/lowCAM); Tysdal et al. 1986 (SAN in MT); Macrostrat (TUR/CON); Bertog 2002 (into lowCAM in MT); COSUNA (TUR/CON)
WY	Fox Hills SS	MAA	Heaton 1950 (MAA); Stephenson & Reeside 1938 (MAA in Great Plains); Tibert et al. 2009 (MAA in N-Plains); Nichols & Jacobson 1982 (MAA); Finn 2005 (MAA); Roberts et al. 2005 (MAA); Finn & Johnson 2005 (MAA); Lehman 1987 (MAA); Mederos et al. 2005 (MAA); Carvajal & Steel 2009 (MAA); Hicks et al. 1999 (MAA); Martinsen et al. 1999 (lowMAA); Willis et al. 1999 (MAA); Liu et al. 2005 (MAA); Johnson et al. 2005 (MAA); USGS DB (MAA); Asquith 1970 (MAA); Hicks et al. 1995 (MAA); Macrostrat (CAM/MAA); Gill & Cobban 1966 (lowMAA); Cobban & Larson 1997 (upCAM/lowMAA); Martinsen 2003 (MAA); Brain 1993 (lowMAA);

			Blackstone 1993 (MAA); Krystinik & DeJarnett 1995 (MAA); COSUNA (CAM/MAA)
WY	Frontier Fm	CEN-CON	Heaton 1950 (CON); Tibert et al. 2009 (CON in northern Plains); Wiltchko & Dorr 1983 (TUR/CON); Nichols & Jacobson 1982 (CEN/TUR); Finn 2005 (CEN-CON); DeCelles & Cavazza 1999 (CEN/TUR); Kirschbaum & Roberts 2005 (CEN/TUR); Mederos et al. 2005 (CEN/TUR); Merewether et al. 2007 (CEN/TUR); Miller 1977 (into CAM); Oboh-Ikuenobe et al. 2007 (CEN to start); Ryer 1993 (CEN-CON); Swift et al. 1985 (TUR/CON in central Rockies); Yang & Miall 2009 (CEN/TUR in MT); Barlow & Haun 1966 (CEN/TUR); Bhattacharya & Willis 2001 (CEN/TUR); Hicks et al. 1999 (into SAN); Lui & Nummedal 2004 (CEN/TUR); Willis et al. 1999 (CEN/TUR); Winn 1989 (CEN/TUR); Liu et al. 2005 (CEN); Johnson et al. 2005 (CEN-CON); Schmitt & Steidtmann 1990 (CEN/TUR); USGS DB (ALB-CON); Asquith 1970 (CEN/TUR); Finn 2010 (CEN-CON); Macrostrat (TUR "SS" or ALB-SAN "Fm"); Martinsen 2003 (CEN/TUR); Martinson et al. 1998 (TUR/CON); COSUNA (ALB/CEN); Cobban & Reeside 1952b (CEN-CON); Nichols & Sweet 1993 (CEN/TUR); Finn & Johnson 2005 (CEN-CON); Lee et al. 2005 (CEN/TUR)
WY	Torchlight SS Mbr (Frontier Fm)	CEN	Burk 1953 ("Sand" = early Greenhorn-age = CEN); Merewether et al. 1975 (early?/midCEN); Cobban and Reeside 1952b (CEN)
WY	Wall Crk Mbr (Frontier Fm) (or Cody Sh?)	TUR	Kirschbaum & Roberts 2005 (TUR/CON); USGS DB (upTUR/midCON); Dyman & Condon 2007 (CEN/TUR); Ryer 1993 (midTUR/CON); Bhattacharya & Willis 2001 (TUR); Burk 1953 (equiv to Turner Sandy & Sage Breaks Mbrs/Carlile Sh = TUR); Liu et al. 2005 (upTUR); Merewether et al. 1975 (lower upTUR); Tillman & Almon 1979 (TUR); Winn 1989 (CON); Martinsen 2003 (TUR); Merewether et al. 2007 (TUR); Lee et al. 2007 (upTUR); Vakarelov & Bhattacharya 2009 (TUR); Gani & Bhattacharya 2007 (TUR); Gani et al. 2008 (TUR); Tomasso et al. 2010 (TUR); Sadeque 2006 (upTUR); Lee et al. 2005 (TUR); Merewether & Claypool 1980 (upTUR); Cobban & Reeside 1952b (TUR)

WY	Greenhorn Fm	CEN/TUR	Kirkland et al. 1999 (CEN/TUR); Stephenson & Reeside 1938 (TUR in Great Plains); Tibert et al. 2009 (CEN/TUR in northern Plains); Nichols & Jacobson 1982 (CEN/TUR); Swift et al. 1985 (CEN/TUR in central Rockies); Yang & Miall 2009 (TUR in northern Great Plains); Winn 1989 (CEN/TUR); Liu et al. 2005 (CEN/TUR); USGS DB (CEN/TUR); Cobban 1984 (CEN/TUR); Macrostrat (CEN/TUR); Cobban & Larson 1997 (upCEN/lowTUR); Cobban et al. 1959 (CEN/TUR); COSUNA (CEN)
WY	Harebell Fm	MAA	Wiltchko & Dorr 1983 (CAM/MAA Harebell "equivalent"); Lehman 1987 (MAA); Hicks et al. 1999 (MAA); Kaufman 1973 (MAA); Harris et al. 1996 (MAA); Lockley et al. 2003 (MAA); Love 1956 ("very Late Cret"); Schmitt & Steidtmann 1990 (MAA); Hicks et al. 1995 (CAM/MAA); Macrostrat (MAA); COSUNA (MAA); NONMARINE
WY	Lance Fm	MAA	Stephenson & Reeside 1938 (DAN in Great Plains & MT); Wiltchko & Dorr 1983 (MAA); Finn 2005 (MAA); Finn & Johnson 2005 (MAA); Lehman 1987 (MAA); Mederos et al. 2005 (MAA); Carvajal & Steel 2009 (MAA); Hicks et al. 1999 (MAA); Martinsen et al. 1999 (lowMAA); Willis et al. 1999 (MAA); Lockley et al. 2003 (MAA); Liu et al. 2005 (MAA); Johnson et al. 2005 (MAA); USGS DB (MAA+); Asquith 1970 (MAA); Hicks et al. 1995 (MAA); Becker et al. 2009 (MAA); Finn 2010 (MAA); Macrostrat (MAA); Gill & Cobban 1966 (upMAA); Martinsen 2003 (MAA); Blackstone 1993 (equiv to Medicine Bow = MAA); Krystinik & DeJarnett 1995 (MAA); COSUNA (MAA); NONMARINE
WY	Landslide Creek Fm	CAM/MAA	Tysdal & Nichols 1991 (<i>Scaphites hippocrepis</i> I thru <i>Baculites asperiformis</i> zones = low/midCAM); Lehman 1987 (MAA); Macrostrat (MAA); COSUNA (MAA); NONMARINE
WY	Lewis Sh	CAM/MAA	Heaton 1950 (CAM/MAA); Finn 2005 (MAA); Roberts et al. 2005 (MAA); Finn & Johnson 2005 (CAM/MAA); Haun 1961 (CAM/MAA); Mederos et al. 2005 (MAA); Miller 1977 (CAM/MAA); Carvajal & Steel 2009 (MAA); Martinsen et al. 1999 (lowMAA); Willis et al. 1999 (CAM/MAA); Liu et al. 2005 (up-mostCAM/MAA); Johnson et al. 2005 (CAM/MAA); USGS DB (upCAM/lowMAA); Asquith 1970 (CAM/MAA); Finn 2010 (CAM); Macrostrat (CON-CAM); Martinsen 2003 (up-mostCAM/lowMAA); Uroza 2008 (upCAM/lowMAA); Brain 1993 (CAM/MAA); Blackstone 1993 (MAA); Krystinik & DeJarnett 1995 (CAM/MAA); COSUNA (CAM)
WY	Dad SS Mbr Lewis Sh	MAA	USGS DB (lowMAA); Finn & Johnson 2005 (MAA); Johnson et al. 2005a,b (MAA); Dymann & Condon 2007 (MAA); Carvajal & Steel 2009 (MAA); Fox 1971 (up-mostCAM/MAA); Perman 1990 (lowMAA); Daly 1997 (equiv to Fox Hills SS = MAA); Brain 1993 (lowMAA)

WY	Lance Fm	MAA	Stephenson & Reeside 1938 (DAN in MT & Great Plains); Wiltshko & Dorr 1983 (MAA); Finn 2005 (MAA); Lehman 1987 (MAA); Mederos et al. 2005 (MAA); Carvajal & Steel 2009 (MAA); Hicks et al. 1999 (MAA); Martinsen et al. 1999 (lowMAA); Willis et al. 1999 (MAA Lance); Liu et al. 2005 (MAA); Johnson et al. 2005 (MAA); USGS DB (MAA); Asquith 1970 (MAA Lance); Hicks et al. 1995 (MAA); Finn 2010 (MAA); Macrostrat (MAA); Martinsen 2003 (MAA); Blackstone 1993 (MAA); Krystinik & DeJarnett 1995 (MAA); COSUNA (MAA); NONMARINE
WY	Meeteetse Fm	CAM/MAA	Heaton 1950 (MAA); Wiltshko & Dorr 1983 (CAM/MAA); Hicks et al. 1999 (CAM/MAA); Harris et al. 1996 (CAM); Stockey et al. 2007 (up-mostCAM); Schmitt & Steidtmann 1990 (CAM); USGS DB (lowMAA); Hicks et al. 1995 (CAM/MAA); Miller et al. 1965 (CAM/MAA); Keefer 1965 (CAM/MAA); Rich 1958 (CAM/MAA); Finn 2010 (CAM/MAA); Macrostrat (CAM/MAA); COSUNA (CAM/MAA); NONMARINE
WY	Medicine Bow Fm	MAA	Haun 1961 (MAA, Medicine Bow = what he calls Lance Fm); Lillegraven & Eberle 1999 (MAA); Secord 1998 (MAA); Wroblewski 2004 (MAA); Perman 1990 (MAA); Fox 1971 (upMAA); Fox 1971 (MAA); Wilson et al. 2001 (MAA); Aydinian 2008 (MAA); Dymann & Condon 2007 (MAA); Lillegraven et al. 2004 (MAA); Macrostrat (MAA); Brain 1993 (lowMAA); Blackstone 1993 (MAA); COSUNA (MAA); NONMARINE
WY	Mesaverde Fm/Grp	CAM	Heaton 1950 (CAM/MAA Mesaverde Grp); Wiltshko & Dorr 1983 (CAM Mesaverde SS); Finn 2005 (CAM Mesaverde Grp); Roberts et al. 2005 (CAM/MAA); Finn & Johnson 2005 (CAM); Mederos et al. 2005 (CAM/MAA); Miller 1977 (CAM/MAA); Demar & Breithaupt 2006 (CAM); Martinsen et al. 1999 (CAM/lowMAA); Willis et al. 1999 (CAM); Harris et al. 1996 (CAM); Johnson et al. 2005 (CAM); Schmitt & Steidtmann 1990 (CAM); USGS DB (SAN/CAM); Finn 2010 (CAM); Macrostrat (TUR-MAA); Jinnah et al. 2009 (CAM at least in part); Martinsen 2003 (CAM); Brain 1993 (CAM); Krystinik & DeJarnett 1995 (CAM); COSUNA (TUR-CAM Mesaverde Grp); top 1/2 is NONMARINE
WY	Allen Ridge Fm Mesaverde Grp	CAM	USGS DB (upCAM); Dymann & Condon 2007 (CAM; above Steele Sh & below Lewis Sh); Finn & Johnson 2005a,b (CAM); Finn 2005 (CAM); Newman 1981 (equiv to Rock Spgs = CAM); Liu et al. 2005 (73.4-78.5Ma = mid/upCAM); Thomas 1978 (CAM); Mellere 1996 (upCAM); Uroza 2008 (mid/upCAM); Mellere & Steel 1995 (mid/upCAM); Brain 1993 (midCAM); Krystinik & DeJarnett 1995 (midCAM); COSUNA (CON)

WY	Almond Fm (Mesaverde Grp)	CAM/MAA	Heaton 1950 (CAM/MAA Mesaverde Grp); Finn 2005 (CAM/MAA); Finn & Johnson 2005 (CAM); Mederos et al. 2005 (CAM/MAA); Miller 1977 (CAM); Demar & Breithaupt 2006 (CAM Mesaverde Grp); Martinsen et al. 1999 (upCAM/lowestMAA); Gates & Farke 2009 (upCAM/lowMAA); Stockey et al. 2007 (upCAM); Liu et al. 2005 (MAA); Johnson et al. 2005 (CAM); USGS DB (upCAM); Perman 1990 (MAA); Finn 2010 (CAM Mesaverde); Macrostrat (CAM); Martinsen 2003 (upCAM); Uroza 2008 (upCAM/lowMAA); Brain 1993 (upCAM); Krystinik & DeJarnett 1995 (CAM/MAA); COSUNA (CAM)
WY	Blair Fm (Mesaverde Grp)	CAM	Heaton 1950 (CAM/MAA Mesaverde Grp); Finn 2005 (CAM); Loseth et al. 2006 (lowCAM); Finn & Johnson 2005 (CAM); Mederos et al. 2005 (CAM); Miller 1977 (CAM); Demar & Breithaupt 2006 (CAM Mesaverde Grp); Levey 1985 (lateCAM); Lui & Nummedal 2004 (CAM); Martinsen et al. 1999 (lowCAM); Liu et al. 2005 (CAM); Johnson et al. 2005 (CAM); USGS DB (lowCAM); Finn 2010 (CAM Mesaverde); Macrostrat (TUR); Jinnah et al. 2009 (lowCAM); Krystinik & DeJarnett 1995 (lowCAM); COSUNA (TUR)
WY	Ericson SS (Mesaverde Grp)	CAM/MAA	Heaton 1950 (CAM/MAA Mesaverde Grp); Witschko & Dorr 1983 (CAM Ericson); Finn 2005 (CAM); Loseth et al. 2006 (upCAM); DeCelles & Cavazza 1999 (CAM/MAA equiv to Hams Fork Conglomerate in UT); Roberts et al. 2005 (CAM); Finn & Johnson 2005 (CAM); Mederos et al. 2005 (CAM); Miller 1977 (CAM); Demar & Breithaupt 2006 (CAM Mesaverde Grp); Levey 1985 (lateCAM); Lui & Nummedal 2004 (upCAM); Martinsen et al. 1999 (upCAM); Liu et al. 2005 (CAM); Johnson et al. 2005 (CAM); USGS DB (upCAM); Macrostrat (CON/SAN); Jinnah et al. 2009 (mid/upCAM); Martinsen 2003 (mid/upCAM); Uroza 2008 (mid/upCAM); Krystinik & DeJarnett 1995 (mid/upCAM); COSUNA (CON/SAN); predominately NONMARINE
WY	Teapot Fm (Mesaverde Grp)	CAM	Jinnah et al. 2009 (upCAM); Macrostrat (SAN/CAM); Finn & Johnson 2005 (CAM); Johnson et al. 2005a.b (CAM); USGS DB (upCAM); Asquith 1970 (upCAM); Hicks et al. 1995 (upCAM); Hicks et al. 1999 (upCAM); Klug 1992 (72-73Ma = upCAM); Martinsen 2003 (upCAM); Krystinik & DeJarnett 1995 (upCAM); COSUNA (SAN/CAM)
WY	Haystack Mtns Fm (Mesaverde Grp)	CAM	USGS DB (CAM); Finn & Johnson 2005a.b (CAM); Finn 2005 (CAM); Dymann & Condon 2007 (CAM); Liu et al. 2005 (midCAM); Mellere 1996 (CAM); Macrostrat (TUR/CON); Uroza 2008 (CAM); Mellere & Steel 1995 (CAM); Mellere & Steel 2000 (CAM); Brain 1993 (low/midCAM); Krystinik & DeJarnett 1995 (midCAM); COSUNA (TUR/CON)
WY	Espy Tongue (Haystack Mtns Fm) (Mesaverde Grp) (or of Steele Sh)	CAM	USGS DB (CAM); Johnson et al. 2005 (CAM)

WY	Deep Crk SS (Haystack Mtns Fm) (or Steele Sh) (or Cody Sh)	CAM	USGS DB (CAM); Finn & Johnson 2005 (CAM); Johnson et al. 2005a,b (CAM); Mellere 1996 (upCAM); Mellere & Steel 1995 (midCAM)
WY	Hatfield SS (Haystack Mtns Fm)	CAM	USGS DB (CAM); Finn & Johnson 2005 (CAM); Johnson et al. 2005a,b (CAM); Thomas 1978 (equiv to Allen Ridge = CAM); Mellere 1996 (upCAM); Uroza 2008 (midCAM); Mellere & Steel 1995 (midCAM); Mellere & Steel 2000 (CAM); Brain 1993 (<i>Baculites asperiformis</i> zone = midCAM); Krystinik & DeJarnett 1995 (midCAM)
WY	O'Brien Sprg (Haystack Mtns Fm)	CAM	USGS DB (lowCAM); Finn & Johnson 2005 (CAM); Johnson et al. 2005a,b (CAM); Mellere 1996 (lowCAM); Uroza 2008 (low/midCAM); Mellere & Steel 1995 (midCAM); Brain 1993 (low/midCAM); Krystinik & DeJarnett 1995 (low/midCAM)
WY	Tapers Ranch (Haystack Mtns Fm)	lowCAM	USGS DB (lowCAM); Johnson et al. 2005a,b (CAM); Mellere 1996 (lowCAM); Uroza 2008 (lowCAM); Mellere & Steel 1995 (lowCAM); Brain 1993 (lowCAM); Krystinik & DeJarnett 1995 (lowCAM)
WY	Rock Springs Fm (Mesaverde Grp)	CAM	Heaton 1950 (CAM/MAA Mesaverde Grp); Finn 2005 (CAM); Loseth et al. 2006 (upCAM); Roberts et al. 2005 (CAM); Mederos et al. 2005 (CAM); Miller 1977 (CAM); Demar & Breithaupt 2006 (CAM Mesaverde Grp); Levey 1985 (lateCAM); Lui & Nummedal 2004 (CAM); Martinsen et al. 1999 (lowCAM); Liu et al. 2005 (CAM); Johnson et al. 2005 (CAM); USGS DB (CAM); Finn 2010 (CAM Mesaverde); Macrostrat (TUR); Jinnah et al. 2009 (low/midCAM); Martinsen 2003 (low/midCAM); COSUNA (TUR)
WY	Mowry Sh	ALB/CEN	Heaton 1950 (CEN/TUR); Kirkland et al. 1999 (ALB/CEN); Stephenson & Reeside 1938 (CEN in MT); Tibert et al. 2009 (CEN in northern Plains); Wiltchko & Dorr 1983 (ALB/CEN); Nichols & Jacobson 1982 (ALB); Finn 2005 (CEN); Oboh-Ikuenobe et al. 2007 (lowCEN); Ryer 1993 (upALB); Swift et al. 1985 (ALB/CEN in central Rockies); Yang & Miall 2009 (ALB/CEN in northern Great Plains); Bhattacharya & Willis 2001 (into CEN); Willis et al. 1999 (ALB/CEN); Schmitt & Steidtmann 1990 (ALB); USGS DB (lowCEN); Finn 2010 (ALB/CEN); Macrostrat (APT-CEN "Sh/CO Grp", ALB-CEN "Fm/CO Grp"); Cobban & Larson 1997 (lowCEN); Cobban et al. 1959 (ALB); Martinsen 2003 (CEN); COSUNA (APT/ALB)

WY	Niobrara Fm	CON-CAM	Heaton 1950 (CON-CAM); Stephenson & Reeside 1938 (CON/SAN in Great Plains); Tibert et al. 2009 (CON-CAM in N-Plains); Nichols & Jacobson 1982 (CON/SAN); Finn 2005 (CON/SAN); Finn & Johnson 2005 (CON/SAN); Merewether et al. 2007 (CON start); Frerichs et al. 1975 (TUR-CAM); Hicks et al. 1999 (into SAN/CAM); Lui & Nummedal 2004 (CON/SAN); Winn 1989 (CON start); Liu et al. 2005 (CON/SAN); Johnson et al. 2005 (TUR-SAN); USGS DB (TUR-CAM); Asquith 1970 (CON-CAM); Hicks et al. 1995 (into CAM); Macrostrat (CEN-SAN); Gill & Cobban 1966 (CON-CAM); Cobban & Larson 1997 (upCON-lowCAM); Cobban et al. 1959 (CON/SAN); Jinnah et al. 2009 (CON-CAM); Martinsen 2003 (CON-CAM); Martinson et al. 1998 (TUR-CAM); Brain 1993 (SAN in part); Krystinik & DeJarnett 1995 (into lowCAM); COSUNA (CEN/TUR); Swift et al. 1985 (SAN/CAM in central rockies)
WY	Pierre Sh	CAM/MAA	Gill & Cobban 1966 (CAM/MAA); Bertog 2010 (CAM to start); Cobban & Larson 1997 (CAM); Cobban et al. 1959 (SAN to start); Jinnah et al. 2009 (mid/upCAM at least in part); Martinsen 2003 (CAM/MAA); COSUNA (CON-CAM)
WY	Ardmore Bentonite (Pierre Sh)		Jinnah et al. 2009 (midCAM - 80-81Ma); Krystinik & DeJarnett 1995 (80.5Ma = low/midCAM)
WY	Upper Un-named Sh (Pierre Sh)	MAA (low)	Gill & Cobban 1966 (lowMAA); Cobban & Larson 1997 (upCAM)
WY	Kara Bentonitic Mbr (Pierre Sh)	CAM (up)	Gill & Cobban 1966 (upCAM)
WY	Lower Un-named Sh (Pierre Sh)	CAM	Gill & Cobban 1966 (upCAM); Bertog 2010 (midCAM to start in Black Hills); Cobban & Larson 1997 (upCAM)
WY	Red Bird Silty Mbr (Pierre Sh)	CAM	Gill & Cobban 1966 (upCAM); Bertog 2010 (midCAM in Black Hills); Cobban & Larson 1997 (midCAM); Asquith 1970 (upCAM)
WY	Mitten Black Sh (Pierre Sh)	CAM	Gill & Cobban 1966 (upCAM); Bertog 2010 (midCAM in Black Hills); Cobban & Larson 1997 (midCAM); Asquith 1970 (upCAM)
WY	Sharon Springs Sh (Pierre Sh)	CAM	Gill & Cobban 1966 (CAM); Bertog 2010 (midCAM in Black Hills); Asquith 1970 (CAM)
WY	Gammon Ferruginous Mbr (Pierre Sh)	CAM (low)	Gill & Cobban 1966 (lowCAM); Bertog et al. 2007 (CAM in MT); Bertog 2010 (lowCAM in Black Hills); Cobban & Larson 1997 (lowCAM); Asquith 1970 (lowCAM); Martinsen 2003 (lowCAM)
WY	Sohare Fm	SAN/CAM	Hicks et al. 1999 (CAM); Harris et al. 1996 (SAN/CAM); Leier 2000 (SAN/CAM); Hunter 1987 (equiv to Hilliard = CON/SAN); COSUNA (TUR/CON "Sohare Sequence"); NONMARINE

WY	Telegraph Creek Fm	SAN/CAM	Stephenson & Reeside 1938 (SAN in Great Plains); Roberts et al. 2005 (CAM in MT); Hicks et al. 1999 (CAM); USGS DB (SAN/CAM); Asquith 1970 (SAN/CAM); Nichols & Sweet 1993 (SAN/CAM in MT); Tysdal & Nichols 1991 (SAN); Hicks et al. 1995 (CAM); Payenberg et al. 2002 (SAN in MT); Payenberg et al. 2003 (SAN in MT); Robinson et al. 1959 (CAM in MT); Finn 2010 (CAM in MT); Macrostrat (TUR-CAM); Bertog 2002 (into lowCAM in MT); Jinnah et al. 2009 (SAN); COSUNA (TUR)
WY	Thermopolis Sh	ALB	Heaton 1950 (CEN); Kirkland et al. 1999 (ALB); Stephenson & Reeside 1938 (CEN in MT); Tibert et al. 2009 (ALB in northern Plains); Wiltschko & Dorr 1983 (ALB); Finn 2005 (ALB); Oboh-Ikuenobe et al. 2007 (ALB/CEN); Willis et al. 1999 (ALB); Schmitt & Steidtmann 1990 (ALB); USGS DB (ALB); Finn 2010 (ALB); Macrostrat (HAUT-ALB); COSUNA (HAUT-BARR)

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Chapter 5. Conclusion

The question of what factors drive evolutionary change has been debated since Darwin first published *On the Origin of Species* (1859). Darwin even wavered on this, considering a much larger role for physical Earth processes in shaping evolution in his initial thinking (e.g., Darwin 1838), yet, these ideas were later considered only in a limited way in the *Origin*, where more focus was given to promoting his evolutionary mechanism of natural selection (Darwin 1859; Gould 2002; Eldredge 2005; Lieberman et al. 2007). Natural selection by definition emphasizes the role of biotic factors in evolution, often in the form of interspecific competition for resources. This view has been championed by many since Darwin, particularly the founders of the Modern Evolutionary Synthesis (e.g., Dobzhansky 1937; Mayr 1942; Simpson 1944) and their “intellectual descendants”, including many recent workers in both extant and extinct evolutionary biology (e.g., MacArthur and Wilson 1972; Van Valen 1973; Vermeij 1987; Jackson and McKinney 1990; Rosenzweig and McCord 1991; Sepkoski et al. 2000).

Biotic factors, however, have not been the sole focus of evolutionary investigations throughout the years. Many studies have demonstrated the importance of abiotic Earth processes in influencing evolution, particularly patterns of diversification (e.g., Raup 1979, 1994; Vrba 1980, 1985; Hallam 1981; Cracraft 1982; Raup and Sepkoski 1982; Knoll 1989, 2012; Allmon and Ross 1990; Knoll et al. 1996; Carroll 2000; Lieberman 2000, 2003a, b; Barnosky 2001; Rothschild and Lister 2003; Stigall Rode and Lieberman 2005a, b; Erwin 2006; Lieberman et al. 2007; Maguire and Stigall 2008; Peters 2008; Myers and Saupe *in press*). The research compiled in this dissertation tested specific hypotheses of both biotic and abiotic factors impacting paleobiogeographic and macroevolutionary patterns of marine taxa during the Late Cretaceous.

To this end, the first two research chapters presented here quantitatively tested for the role of competitive exclusion in extinction selectivity and the impact of geographic range size on patterns of survivorship and invasion potential across a phylogenetically and ecologically diverse set of marine taxa. The results indicate that competitive exclusion was not a driving force in marine vertebrate extinctions. Further, large geographic range was not found to increase survivorship or invasion potential in marine mollusks. These results offer unique insight into common patterns of how species interact with their environment, and each other, in a warmer world.

The final chapter examined the application of ecological niche modeling (ENM) in the fossil record. This chapter provided an in depth discussion of conceptual considerations that are essential to producing quality models of species abiotic requirements used to test hypotheses of the impacts of biotic and abiotic factors on macroevolutionary patterns (e.g., ecological niche stability, breadth, and phylogenetic conservation). This chapter further specified a standardized framework for collection of species occurrence and stratigraphic data and paleoenvironmental reconstruction necessary for applying ENM techniques in the fossil record.

My research aimed to elucidate the ways in which ecology, biogeography, and evolution are interrelated. I used the Late Cretaceous marine fossil record as a laboratory to quantitatively test hypotheses of the impact of biotic vs. abiotic changes mediating speciation, extinction, and distribution patterns. This research integrated tools and concepts from diverse fields in the Earth and evolutionary sciences, including paleobiology, ecology, biogeography, and paleoenvironmental reconstruction. Such a synthetic approach helps provide a comprehensive view of paleobiogeographic and macroevolutionary patterns in marine taxa during the Late

Cretaceous and may offer important clues to inform predictions of species' responses to projected future environmental changes.

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Appendices

Appendix 1-1. PaleoGIS range area reconstructions for each taxon during each stage of the Late Cretaceous. S = range area (km), S* = estimated mean range area calculated by jackknifing (km), SE = standard error, L1 and L2 = 95% confidence bands on S*.

	Cenomanian	Turonian	Coniacian	Santonian	Campanian	Maastrichtian
<i>Cretoxyrhina mantelli</i>						
S	244689	314459	215995	4773	0	0
S*	489336	657508	539695	5673	0	0
SE	212723	260631	214829	0	0	0
L1	21134	112008	78887	5672	0	0
L2	957538	1203008	1000503	5675	0	0
Number of Occurrences	33	30	20	21	0	0
Number of Unique Localities	12	20	15	17	0	0
Percent Deletion for each 'n-1' Jackknife Replicate (%)	8.3	5	6.7	5.9	0	0
<i>Squalicorax falcatus</i>						
S	592794	450817	50150	5008	346	0
S*	1349661	586236	115595	6404	489	0
SE	547638	103871	43388	619	0	0
L1	129523	376105	17452	5025	487	0
L2	2569799	796367	213738	7783	491	0
Number of Occurrences	31	135	16	13	2	0
Number of Unique Localities	11	40	10	11	2	0
Percent Deletion for each 'n-1' Jackknife Replicate (%)	9.1	2.5	10	9.1	50	0
<i>Squalicorax kaupi</i>						
S	0	0	248	81269	1257485	19158
S*	0	0	248	150349	1288483	34369
SE	0	0	0	73370	158316	13704
L1	0	0	0	-8130	940030	-9239
L2	0	0	0	308828	1636936	77976
Number of Occurrences	0	0	1	16	32	4
Number of Unique Localities	0	0	1	14	12	4
Percent Deletion for each 'n-1' Jackknife Replicate (%)	0	0	0	7.1	8.3	25
<i>Platecarpus sp.</i>						
S	0	0	2166	134938	66714	0
S*	0	0	3636	259184	124652	0
SE	0	0	1363	119186	45122	0
L1	0	0	-702	3530	24120	0
L2	0	0	7975	514838	225185	0
Number of Occurrences	0	0	4	15	51	0
Number of Unique Localities	0	0	4	15	11	0

Percent Deletion for each 'n-1' Jackknife Replicate (%)	0	0	25	6.7	9.1	0
<i>Tylosaurus sp.</i>						
S	0	0	74779	256	284026	258
S*	0	0	84512	289	620362	258
SE	0	0	21141	18	205076	0
L1	0	0	38848	210	93112	0
L2	0	0	130176	368	1147612	0
Number of Occurrences	0	0	19	3	9	1
Number of Unique Localities	0	0	14	3	6	1
Percent Deletion for each 'n-1' Jackknife Replicate (%)	0	0	7.1	33.3	16.7	0
<i>Xiphactinus sp.</i>						
S	53781	22796	3277	5898	115958	228
S*	126429	48968	5325	9518	280735	228
SE	44605	15793	1015	2335	95088	0
L1	23570	15091	2508	4473	16770	0
L2	229288	82845	8142	14562	544700	0
Number of Occurrences	13	58	6	16	8	1
Number of Unique Localities	9	15	5	14	5	1
Percent Deletion for each 'n-1' Jackknife Replicate (%)	11.1	6.7	20	7.1	20	0
<i>Ptychodus anonymus</i>						
S	229810	494312	1627	0	0	0
S*	587339	1300755	3028	0	0	0
SE	217879	502172	1	0	0	0
L1	27171	223597	3018	0	0	0
L2	1147507	2377913	3038	0	0	0
Number of Occurrences	10	50	2	0	0	0
Number of Unique Localities	6	15	2	0	0	0
Percent Deletion for each 'n-1' Jackknife Replicate (%)	16.7	6.7	50	0	0	0
<i>Ptychodus mortoni</i>						
S	0	241	636141	41279	262031	0
S*	0	241	1383280	64591	475384	0
SE	0	0	464877	36355	96909	0
L1	0	0	245727	-21388	206366	0
L2	0	0	2520833	150570	744403	0
Number of Occurrences	0	1	11	12	7	0
Number of Unique Localities	0	1	7	8	5	0
Percent Deletion for each 'n-1' Jackknife Replicate (%)	0	0	14.3	12.5	20	0
<i>Ptychodus whipplei</i>						
S	241	954857	248	0	0	0
S*	241	1548376	248	0	0	0
SE	0	466188	0	0	0	0
L1	0	596420	0	0	0	0
L2	0	2500332	0	0	0	0
Number of Occurrences	1	58	1	0	0	0

Number of Unique Localities	1	31	1	0	0	0
Percent Deletion for each 'n-1' Jackknife Replicate (%)	0	3.2	0	0	0	0
<i>Rhinobatos incertus</i>						
S	12126	3445	2258	305	665	0
S*	21260	4333	4289	338	1108	0
SE	9183	344	1	19	0	0
L1	-4232	3239	4282	279	1103	0
L2	46751	5426	4296	398	1114	0
Number of Occurrences	10	28	5	10	4	0
Number of Unique Localities	5	4	2	4	2	0
Percent Deletion for each 'n-1' Jackknife Replicate (%)	20	25	50	25	50	0

Appendix 1-2. Correlation results for range area analysis of all pairwise comparisons. A

Bonferroni correction (Sokal and Rohlf 1995) for multiple comparisons indicates a critical p-value of $p \leq 0.001$ for statistical significance.

Taxon A	Taxon B	Spearman's ρ	p-value	Kendall's τ	p-value
<i>Cretoxyrhina mantelli</i>	<i>Squalicorax falcatus</i>	0.928	0.022	0.828	0.020
<i>Cretoxyrhina mantelli</i>	<i>Squalicorax kaupi</i>	-0.882	0.036	-0.786	0.027
<i>Cretoxyrhina mantelli</i>	<i>Platecarpus</i> sp.	-0.431	0.392	-0.386	0.277
<i>Cretoxyrhina mantelli</i>	<i>Tylosaurus</i> sp.	-0.765	0.097	-0.643	0.070
<i>Cretoxyrhina mantelli</i>	<i>Ptychodus anonymus</i>	0.955	0.025	0.926	0.009
<i>Cretoxyrhina mantelli</i>	<i>Ptychodus mortoni</i>	-0.132	0.789	-0.071	0.841
<i>Cretoxyrhina mantelli</i>	<i>Ptychodus whipplei</i>	0.893	0.042	0.772	0.030
<i>Cretoxyrhina mantelli</i>	<i>Rhinobatos incertus</i>	0.841	0.044	0.690	0.052
<i>Cretoxyrhina mantelli</i>	<i>Xiphactinus</i> sp.	0.174	0.733	0.138	0.697
<i>Squalicorax falcatus</i>	<i>Squalicorax kaupi</i>	-0.812	0.072	-0.690	0.052
<i>Squalicorax falcatus</i>	<i>Platecarpus</i> sp.	-0.334	0.533	-0.298	0.401
<i>Squalicorax falcatus</i>	<i>Tylosaurus</i> sp.	-0.696	0.144	-0.552	0.120
<i>Squalicorax falcatus</i>	<i>Xiphactinus</i> sp.	0.371	0.419	0.333	0.348
<i>Squalicorax falcatus</i>	<i>Ptychodus anonymus</i>	0.880	0.050	0.745	0.036
<i>Squalicorax falcatus</i>	<i>Ptychodus mortoni</i>	-0.116	0.844	-0.138	0.697
<i>Squalicorax falcatus</i>	<i>Ptychodus whipplei</i>	0.759	0.117	0.596	0.093
<i>Squalicorax falcatus</i>	<i>Rhinobatos incertus</i>	0.943	0.003	0.867	0.015
<i>Squalicorax kaupi</i>	<i>Platecarpus</i> sp.	0.770	0.108	0.617	0.082
<i>Squalicorax kaupi</i>	<i>Tylosaurus</i> sp.	0.765	0.097	0.571	0.107
<i>Squalicorax kaupi</i>	<i>Xiphactinus</i> sp.	0.058	0.933	0.000	1.000
<i>Squalicorax kaupi</i>	<i>Ptychodus anonymus</i>	-0.924	0.042	-0.849	0.017
<i>Squalicorax kaupi</i>	<i>Ptychodus mortoni</i>	0.427	0.408	0.357	0.314
<i>Squalicorax kaupi</i>	<i>Ptychodus whipplei</i>	-0.832	0.067	-0.694	0.050
<i>Squalicorax kaupi</i>	<i>Rhinobatos incertus</i>	-0.754	0.106	0.552	0.120
<i>Platecarpus</i> sp.	<i>Tylosaurus</i> sp.	0.524	0.283	0.463	0.192
<i>Platecarpus</i> sp.	<i>Xiphactinus</i> sp.	0.152	0.833	0.149	0.674
<i>Platecarpus</i> sp.	<i>Ptychodus anonymus</i>	-0.613	0.200	-0.583	0.100
<i>Platecarpus</i> sp.	<i>Ptychodus mortoni</i>	0.709	0.142	0.463	0.192
<i>Platecarpus</i> sp.	<i>Ptychodus whipplei</i>	-0.484	0.350	-0.417	0.240
<i>Platecarpus</i> sp.	<i>Rhinobatos incertus</i>	-0.395	0.450	-0.447	0.208
<i>Tylosaurus</i> sp.	<i>Xiphactinus</i> sp.	-0.058	0.933	-0.138	0.697
<i>Tylosaurus</i> sp.	<i>Ptychodus anonymus</i>	-0.678	0.158	-0.540	0.128
<i>Tylosaurus</i> sp.	<i>Ptychodus mortoni</i>	0.662	0.169	0.500	0.159
<i>Tylosaurus</i> sp.	<i>Ptychodus whipplei</i>	-0.462	0.358	0.385	0.277
<i>Tylosaurus</i> sp.	<i>Rhinobatos incertus</i>	-0.522	0.300	-0.414	0.243
<i>Xiphactinus</i> sp.	<i>Ptychodus anonymus</i>	0.213	0.733	0.149	0.674
<i>Xiphactinus</i> sp.	<i>Ptychodus mortoni</i>	0.087	0.861	0.000	1.000
<i>Xiphactinus</i> sp.	<i>Ptychodus whipplei</i>	0.030	1.000	0.000	1.000
<i>Xiphactinus</i> sp.	<i>Rhinobatos incertus</i>	0.543	0.242	0.467	0.189
<i>Ptychodus anonymus</i>	<i>Ptychodus mortoni</i>	-0.185	0.742	-0.077	0.828
<i>Ptychodus anonymus</i>	<i>Ptychodus whipplei</i>	0.936	0.025	0.833	0.019
<i>Ptychodus anonymus</i>	<i>Rhinobatos incertus</i>	0.880	0.050	0.745	0.036
<i>Ptychodus mortoni</i>	<i>Ptychodus whipplei</i>	0.092	0.883	0.077	0.828
<i>Ptychodus mortoni</i>	<i>Rhinobatos incertus</i>	-0.058	0.933	0.000	1.000

<i>Ptychodus whipplei</i>	<i>Rhinobatos incertus</i>	0.786	0.117	0.596	0.093
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Appendix 1-3. Correlation results for range area analysis of all pairwise comparisons using resampled mean range estimated by jackknifing procedure. A Bonferroni correction (Sokal and Rohlf 1995) for multiple comparisons indicates a critical p-value of $p \leq 0.001$ for statistical significance.

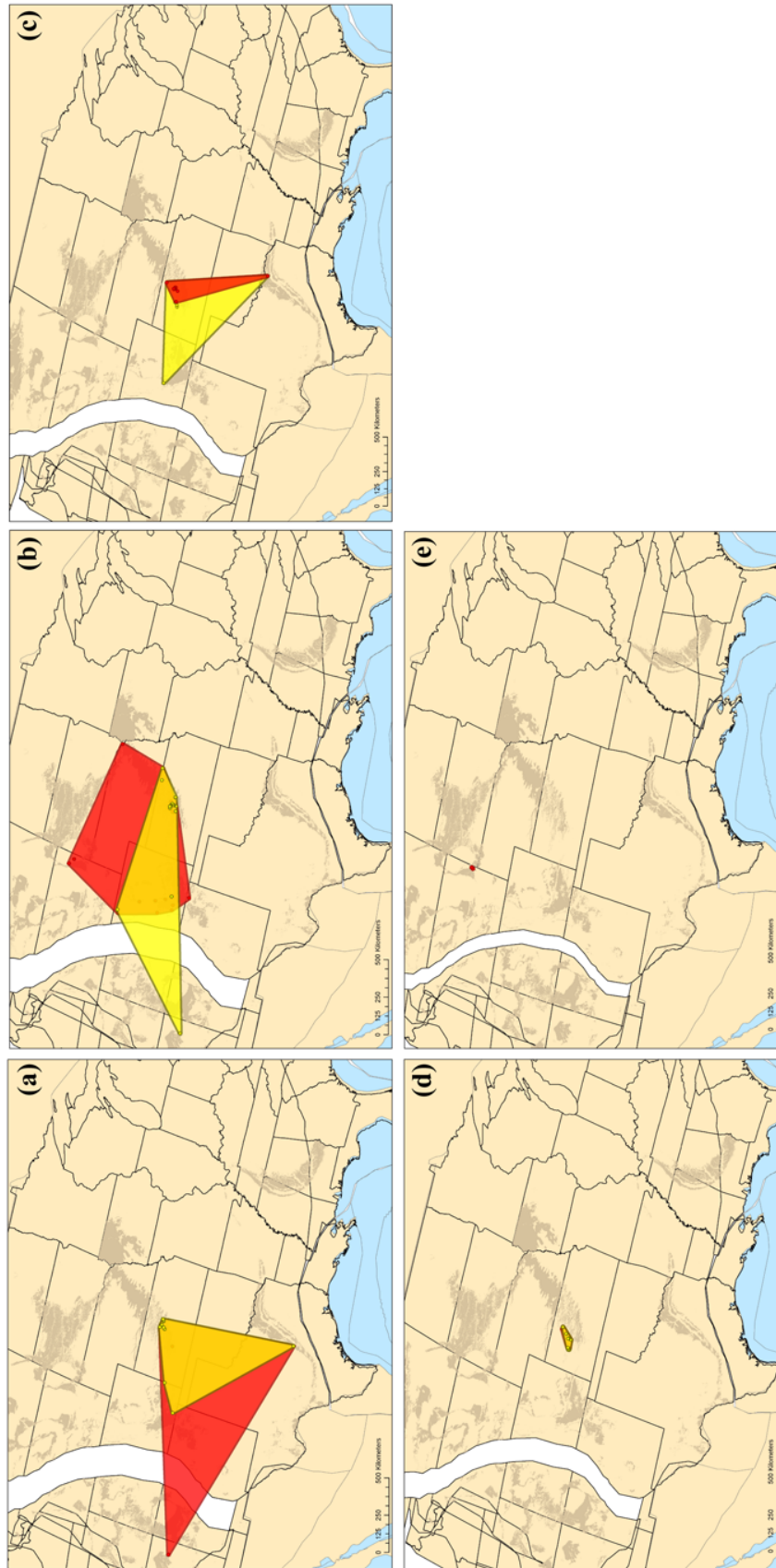
Taxon A	Taxon B	Spearman's ρ	p-value	Kendall's τ	p-value
<i>Cretoxyrhina mantelli</i>	<i>Squalicorax falcatus</i>	0.812	0.072	0.690	0.052
<i>Cretoxyrhina mantelli</i>	<i>Squalicorax kaupi</i>	-0.794	0.081	0.643	0.070
<i>Cretoxyrhina mantelli</i>	<i>Platecarpus</i> sp.	-0.308	0.533	-0.232	0.514
<i>Cretoxyrhina mantelli</i>	<i>Tylosaurus</i> sp.	-0.471	0.342	-0.357	0.314
<i>Cretoxyrhina mantelli</i>	<i>Xiphactinus</i> sp.	0.000	1.000	0.000	1.000
<i>Cretoxyrhina mantelli</i>	<i>Ptychodus anonymus</i>	0.893	0.042	0.772	0.030
<i>Cretoxyrhina mantelli</i>	<i>Ptychodus mortoni</i>	0.132	0.789	0.071	0.841
<i>Cretoxyrhina mantelli</i>	<i>Ptychodus whipplei</i>	0.955	0.025	0.926	0.009
<i>Cretoxyrhina mantelli</i>	<i>Rhinobatos incertus</i>	0.725	0.122	0.552	0.120
<i>Squalicorax falcatus</i>	<i>Squalicorax kaupi</i>	-0.812	0.072	-0.690	0.052
<i>Squalicorax falcatus</i>	<i>Platecarpus</i> sp.	-0.334	0.533	-0.298	0.401
<i>Squalicorax falcatus</i>	<i>Tylosaurus</i> sp.	-0.580	0.244	-0.414	0.243
<i>Squalicorax falcatus</i>	<i>Xiphactinus</i> sp.	0.371	0.420	0.333	0.348
<i>Squalicorax falcatus</i>	<i>Ptychodus anonymus</i>	0.880	0.050	0.745	0.036
<i>Squalicorax falcatus</i>	<i>Ptychodus mortoni</i>	-0.116	0.844	-0.138	0.697
<i>Squalicorax falcatus</i>	<i>Ptychodus whipplei</i>	0.759	0.117	0.596	0.093
<i>Squalicorax falcatus</i>	<i>Rhinobatos incertus</i>	0.943	0.003	0.867	0.015
<i>Squalicorax kaupi</i>	<i>Platecarpus</i> sp.	0.770	0.108	0.617	0.082
<i>Squalicorax kaupi</i>	<i>Tylosaurus</i> sp.	0.824	0.053	0.714	0.044
<i>Squalicorax kaupi</i>	<i>Xiphactinus</i> sp.	0.058	0.933	0.000	1.000
<i>Squalicorax kaupi</i>	<i>Ptychodus anonymus</i>	-0.924	0.042	-0.849	0.017
<i>Squalicorax kaupi</i>	<i>Ptychodus mortoni</i>	0.427	0.408	0.357	0.314
<i>Squalicorax kaupi</i>	<i>Ptychodus whipplei</i>	-0.832	0.067	-0.694	0.050
<i>Squalicorax kaupi</i>	<i>Rhinobatos incertus</i>	-0.754	0.106	0.552	0.120
<i>Platecarpus</i> sp.	<i>Tylosaurus</i> sp.	0.770	0.108	0.617	0.082
<i>Platecarpus</i> sp.	<i>Xiphactinus</i> sp.	0.152	0.833	0.149	0.674
<i>Platecarpus</i> sp.	<i>Ptychodus anonymus</i>	-0.613	0.200	-0.583	0.100
<i>Platecarpus</i> sp.	<i>Ptychodus mortoni</i>	0.709	0.142	0.463	0.192
<i>Platecarpus</i> sp.	<i>Ptychodus whipplei</i>	-0.484	0.350	-0.417	0.240
<i>Platecarpus</i> sp.	<i>Rhinobatos incertus</i>	-0.395	0.450	-0.447	0.208
<i>Tylosaurus</i> sp.	<i>Xiphactinus</i> sp.	0.058	0.933	0.000	1.000
<i>Tylosaurus</i> sp.	<i>Ptychodus anonymus</i>	-0.678	0.158	-0.540	0.128
<i>Tylosaurus</i> sp.	<i>Ptychodus mortoni</i>	0.809	0.064	0.643	0.070
<i>Tylosaurus</i> sp.	<i>Ptychodus whipplei</i>	-0.462	0.358	0.386	0.277
<i>Tylosaurus</i> sp.	<i>Rhinobatos incertus</i>	-0.464	0.372	-0.276	0.437
<i>Xiphactinus</i> sp.	<i>Ptychodus anonymus</i>	0.213	0.733	0.149	0.674
<i>Xiphactinus</i> sp.	<i>Ptychodus mortoni</i>	0.087	0.861	0.000	1.000
<i>Xiphactinus</i> sp.	<i>Ptychodus whipplei</i>	0.030	1.000	0.000	1.000
<i>Xiphactinus</i> sp.	<i>Rhinobatos incertus</i>	0.543	0.242	0.467	0.189
<i>Ptychodus anonymus</i>	<i>Ptychodus mortoni</i>	-0.185	0.742	-0.077	0.828
<i>Ptychodus anonymus</i>	<i>Ptychodus whipplei</i>	0.936	0.025	0.833	0.019

<i>Ptychodus anonymus</i>	<i>Rhinobatos incertus</i>	0.880	0.050	0.745	0.036
<i>Ptychodus mortoni</i>	<i>Ptychodus whipplei</i>	0.092	0.883	0.077	0.828
<i>Ptychodus mortoni</i>	<i>Rhinobatos incertus</i>	-0.058	0.933	0.000	1.000
<i>Ptychodus whipplei</i>	<i>Rhinobatos incertus</i>	0.786	0.117	0.596	0.093

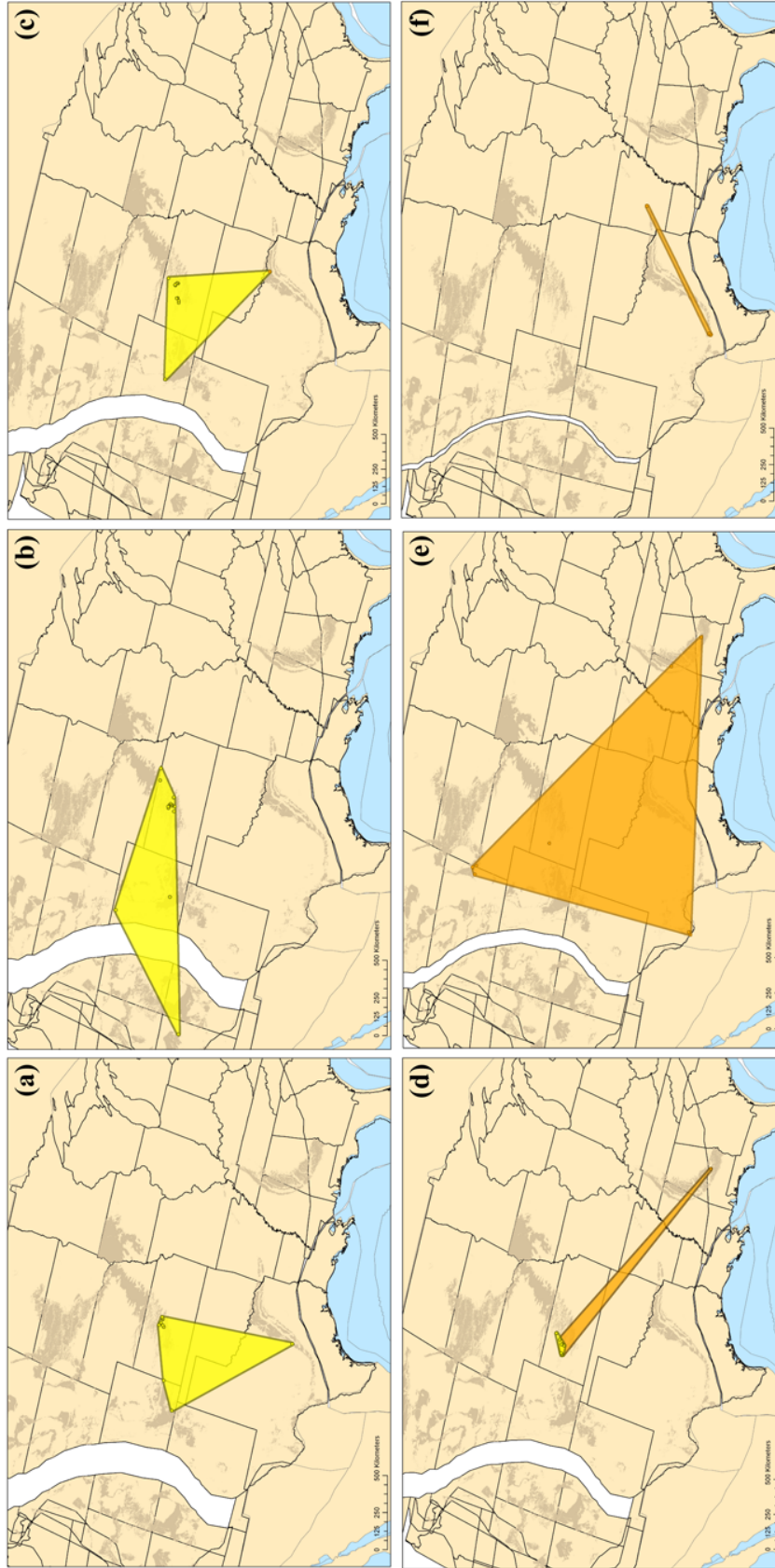
Appendix 1-4. Correlation results between number of unique geographic localities sampled and reconstructed geographic range size for each stage during the Late Cretaceous using resampled mean range estimated by jackknifing procedure. A Bonferroni correction (Sokal and Rohlf 1995) for multiple comparisons indicates a critical p-value of $p \leq 0.007$ for statistical significance.

Coniacian* represents the correlation between number of unique geographic localities and reconstructed range size after removing taxa that either originate or go extinct during this stage.

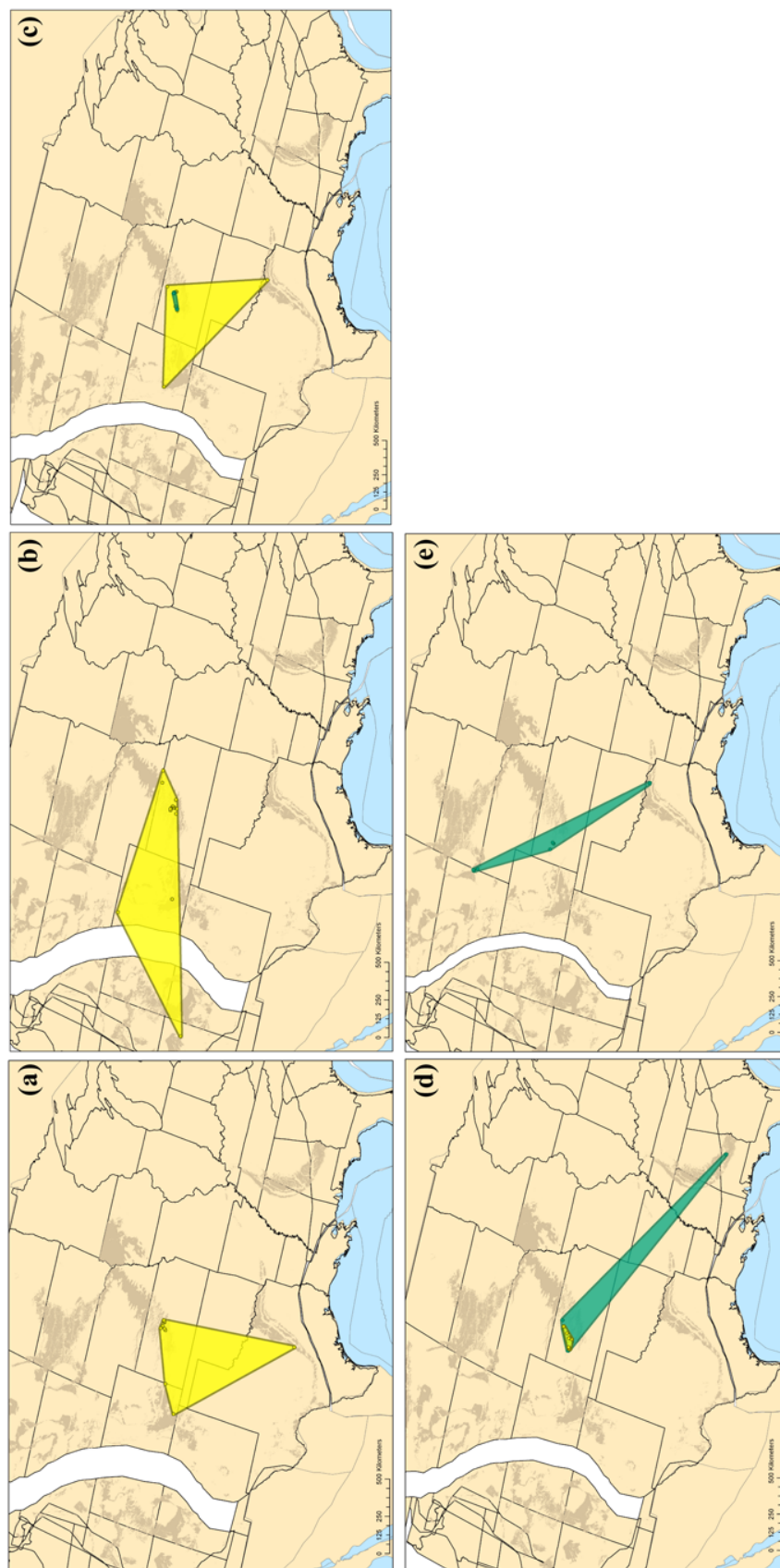
Stage	Spearman's ρ	p-value	Kendall's τ	p-value
Cenomanian	0.714	0.136	0.600	0.091
Turonian	0.703	0.086	0.586	0.065
Coniacian	0.893	0.001	0.759	0.002
Coniacian*	0.700	0.2333	0.600	0.142
Santonian	0.551	0.163	0.473	0.101
Campanian	0.764	0.056	0.651	0.040
Maastrichtian	0.866	0.667	0.817	0.201
Total (combined)	0.785	0.015	0.600	0.016



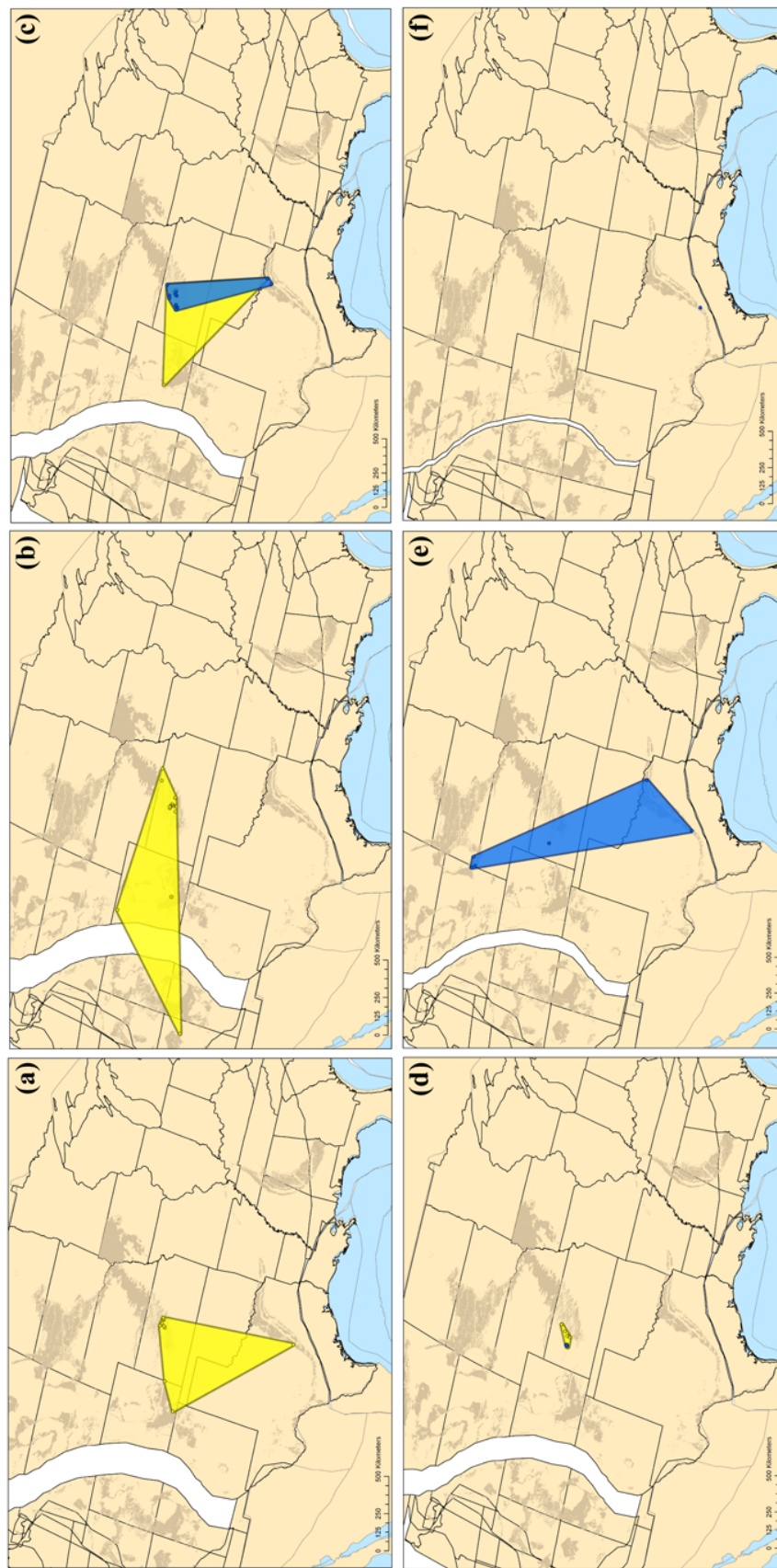
Appendix 1-5. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Cretoxyrhina mantelli* (yellow) and *Squalicorax falcatus* (red) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



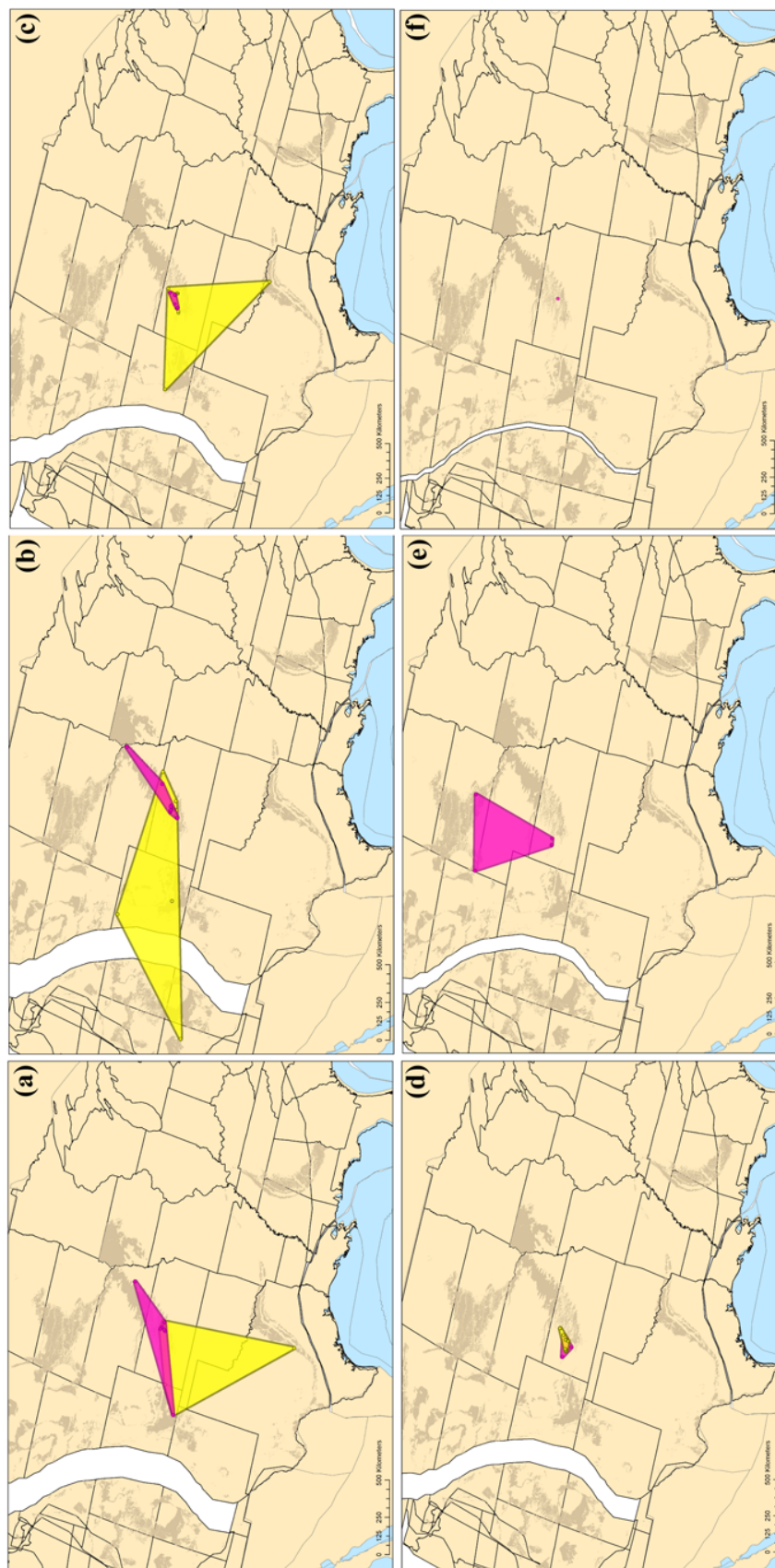
Appendix 1-6. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Cretoxyrhina mantelli* (yellow) and *Squalicorax kaupi* (orange) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



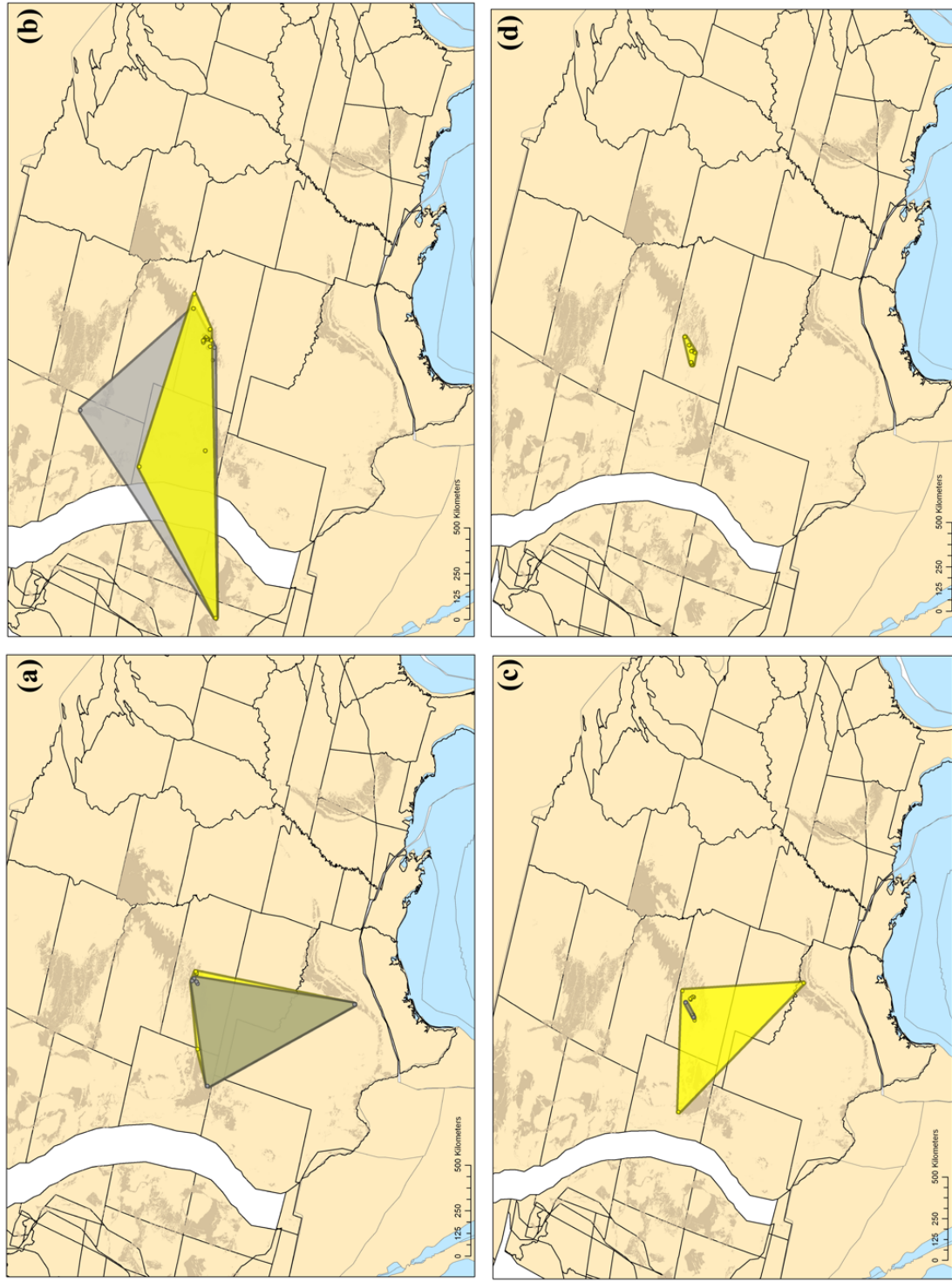
Appendix 1-7. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Cretoxyrhina mantelli* (yellow) and *Platecarpus* sp. (dark green) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



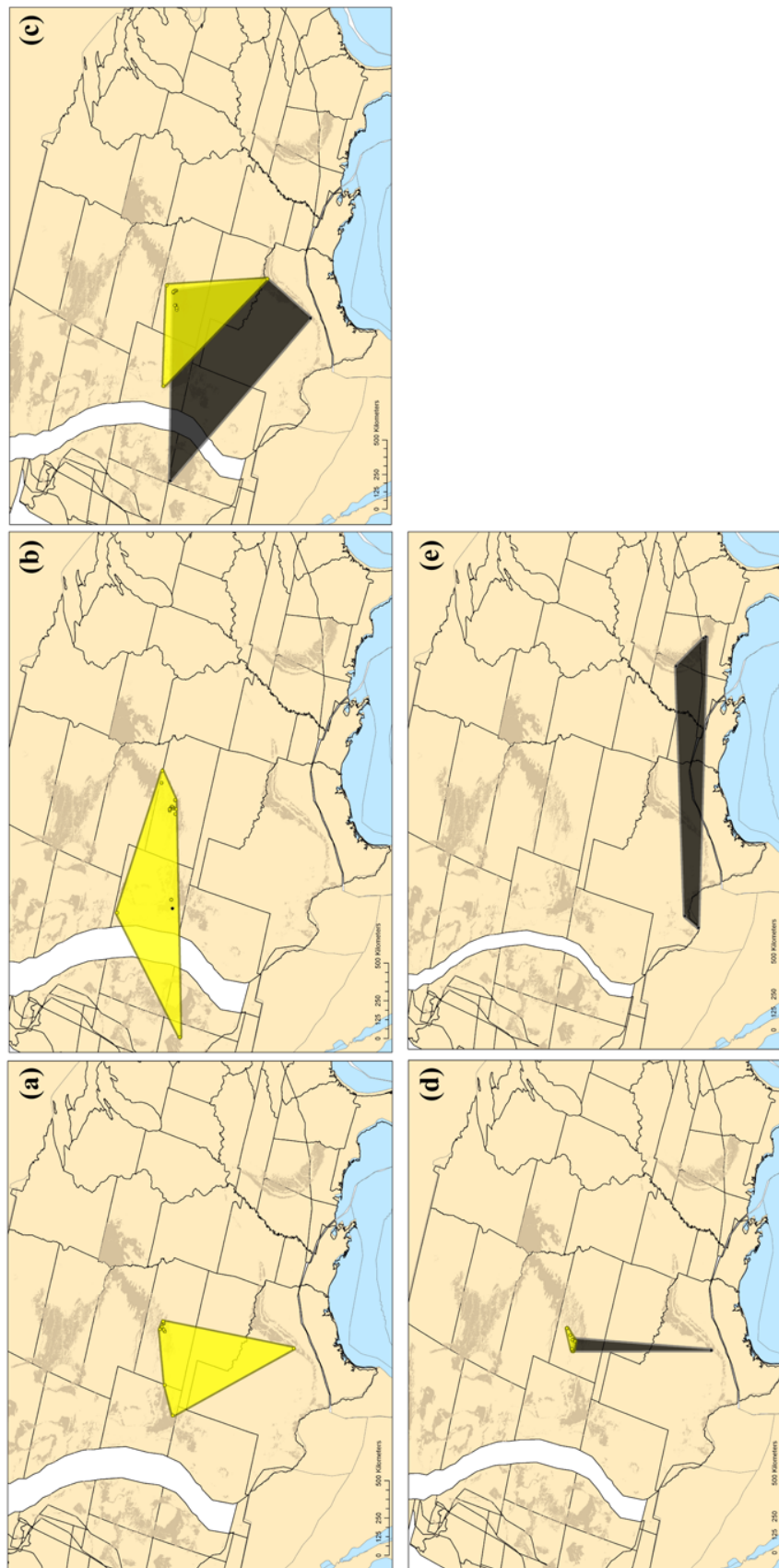
Appendix 1-8. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Cretoxyrhina mantelli* (blue) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



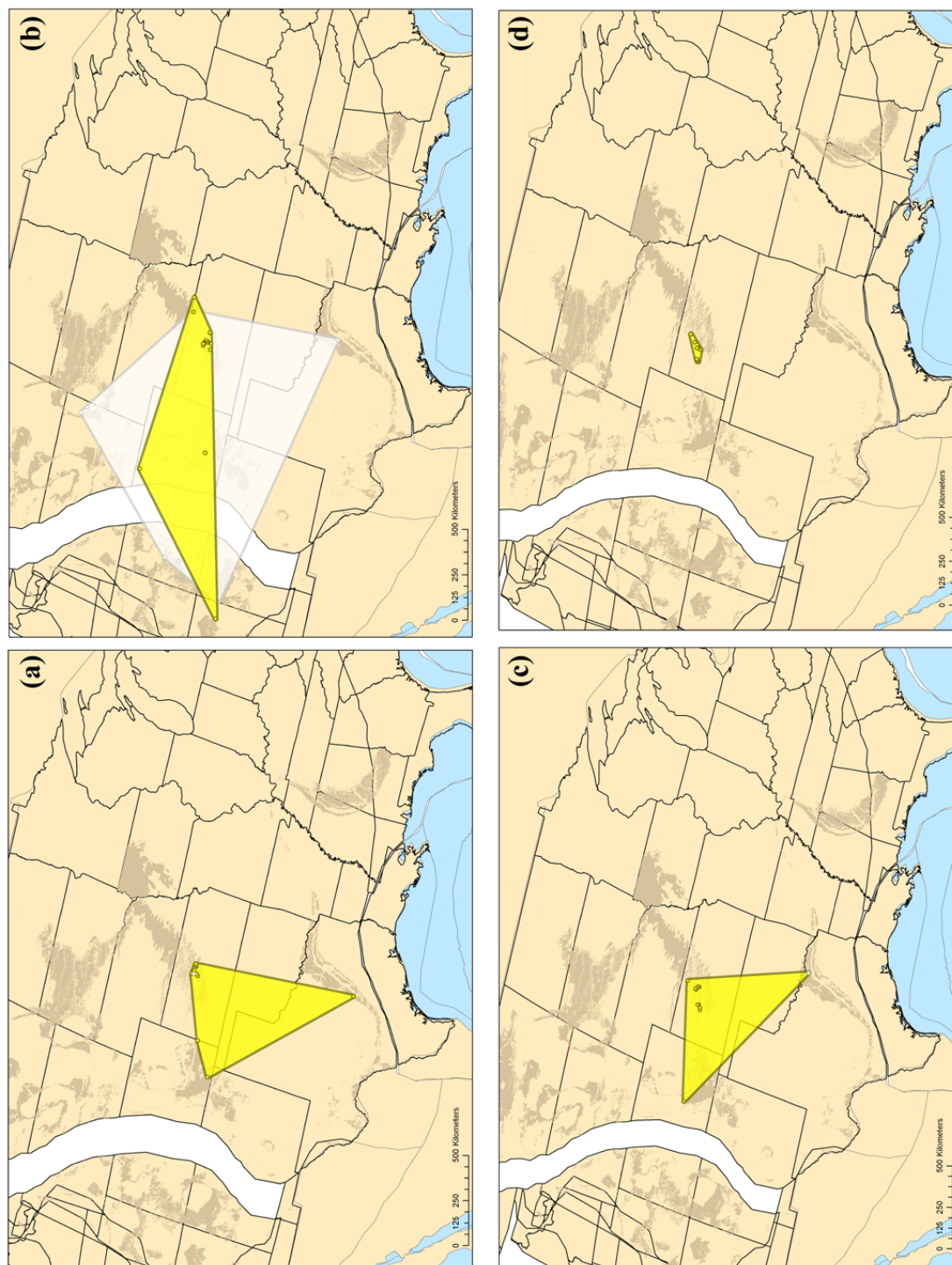
Appendix 1-9. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Cretoxyrhina mantelli* (yellow) and *Xiphactinus* sp. (pink) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



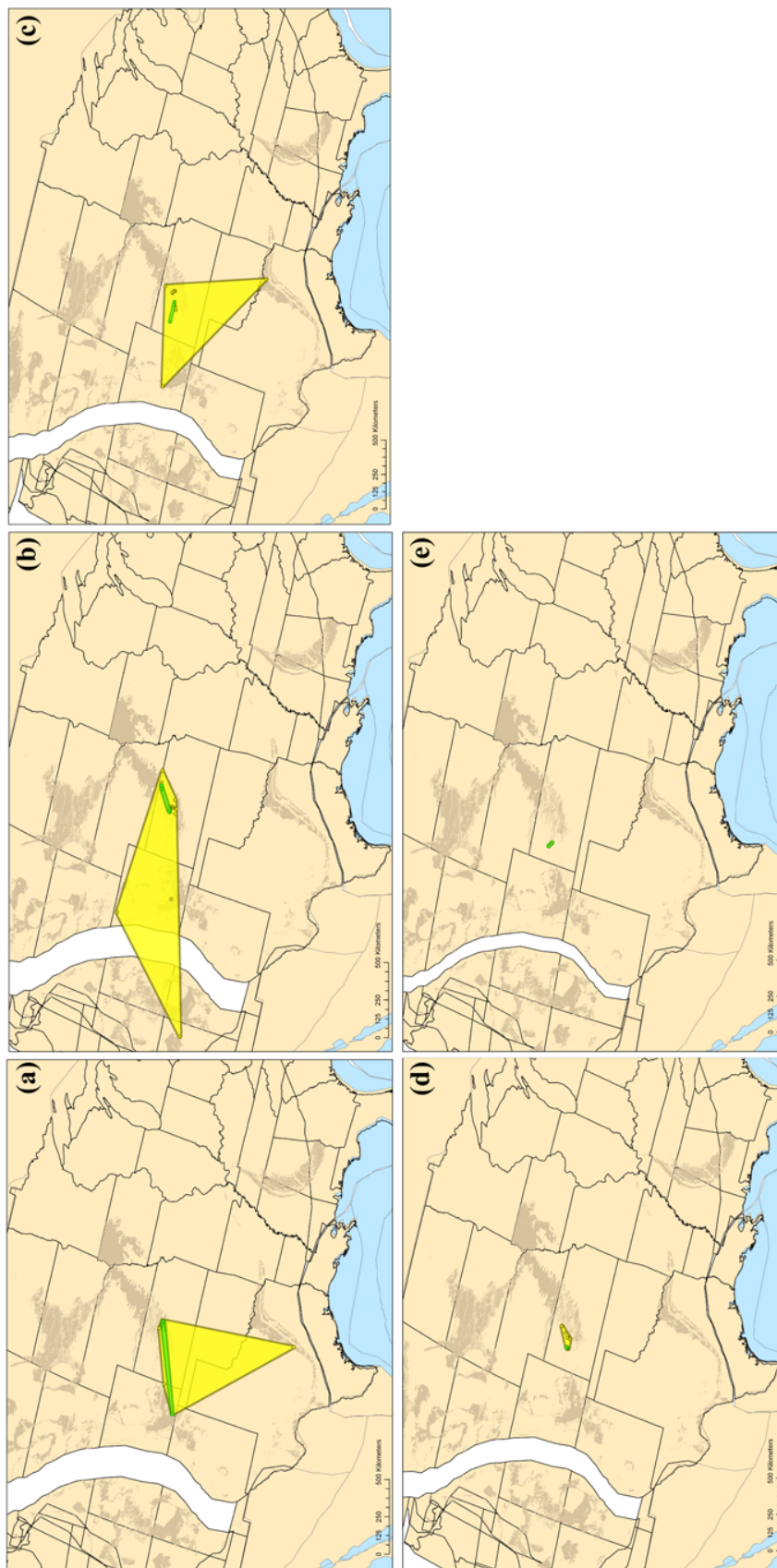
Appendix 1-10. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Cretoxyrhina mantelli* (yellow) and *Pitychodus anonymus* (grey) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



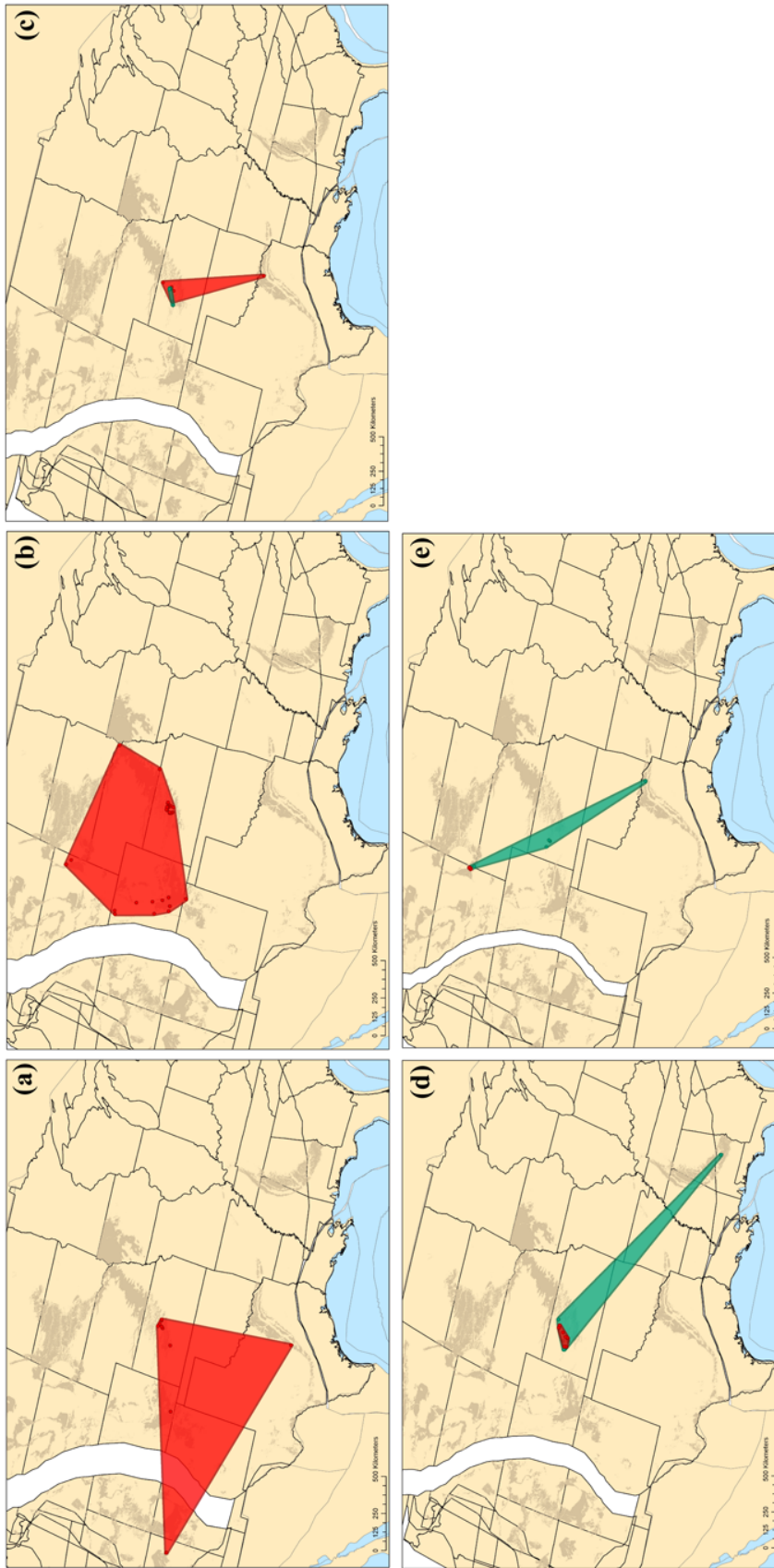
Appendix 1-11. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Cretoxyrhina mantelli* (yellow) and *Ptychodus mortoni* (black) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



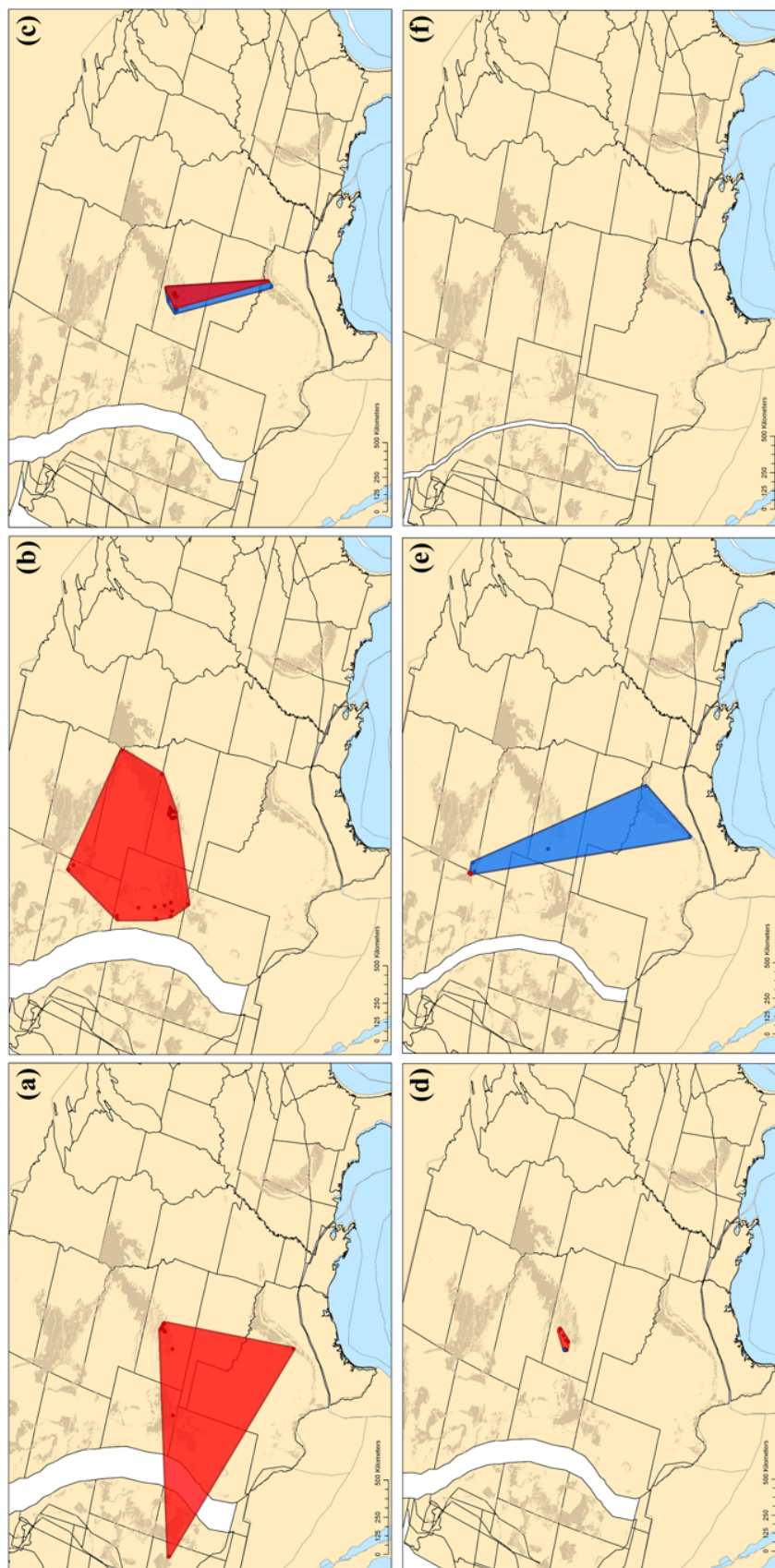
Appendix 1-12. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Cretoxyrhina mantelli* (yellow) and *Ptychodus whipplei* (white) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



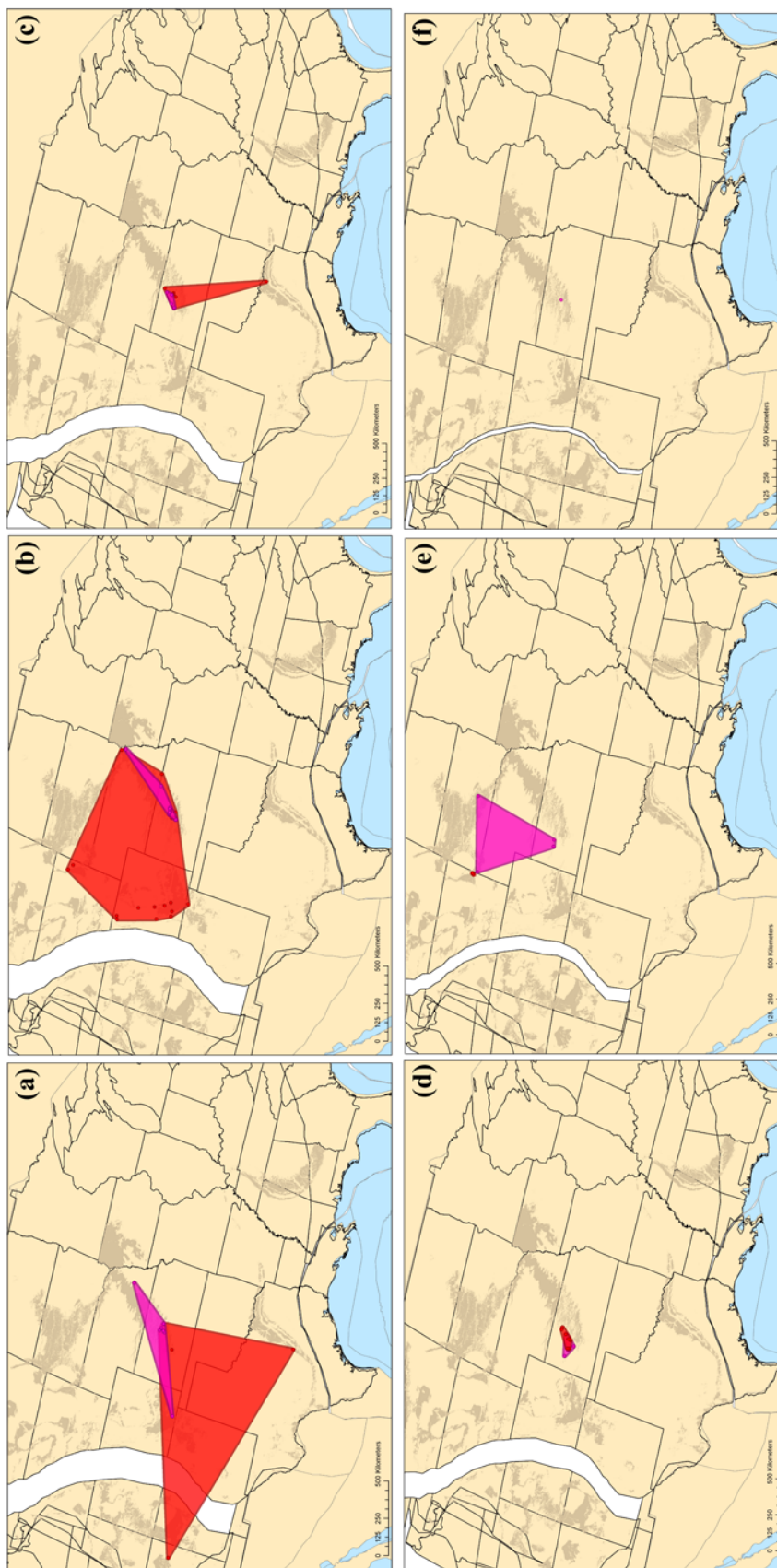
Appendix 1-13. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Cretoxyrhina mantelli* (yellow) and *Rhinobatos incertus* (light green) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



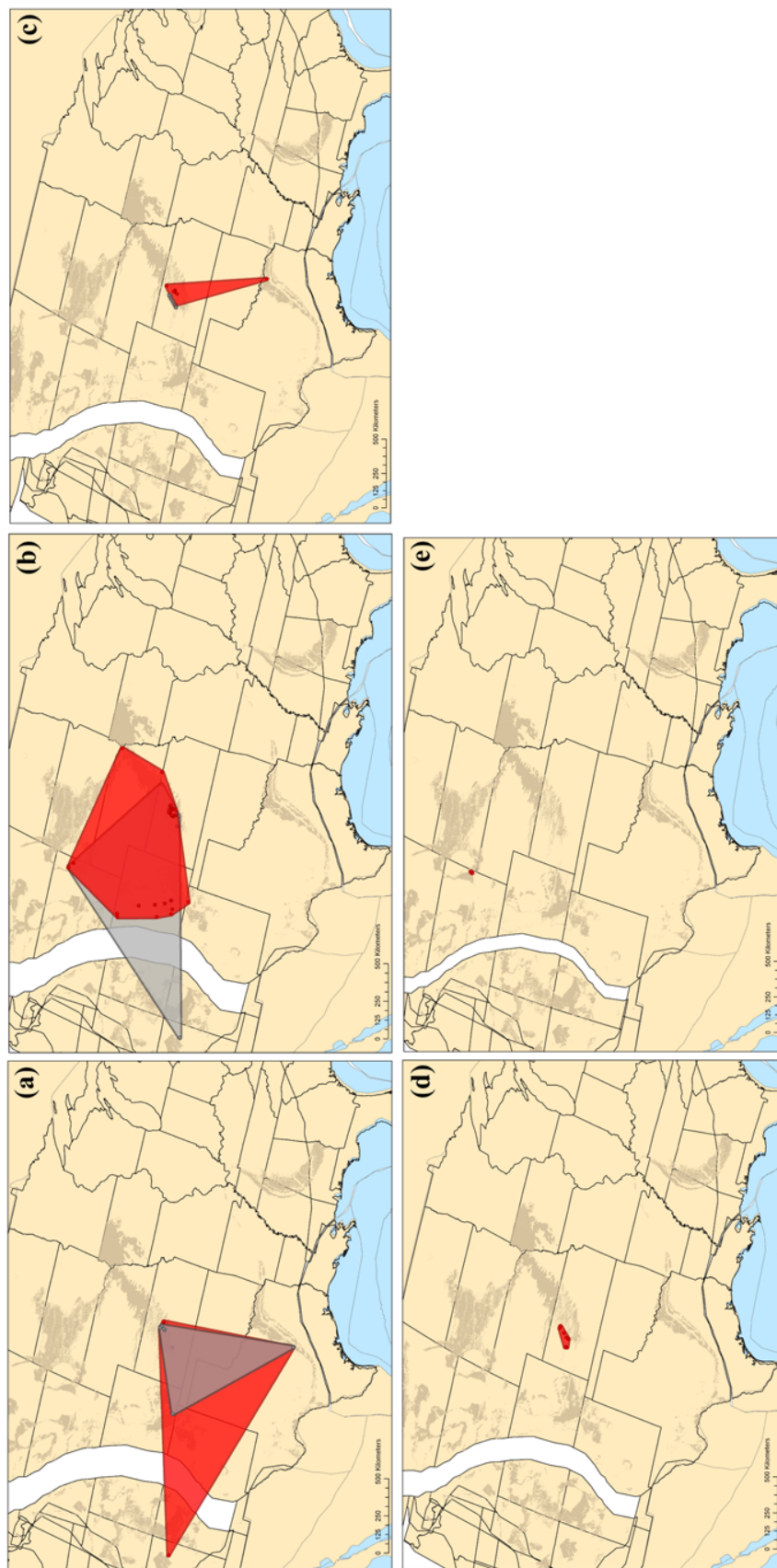
Appendix 1-14. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Squalicorax falcatus* sp. (dark green) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



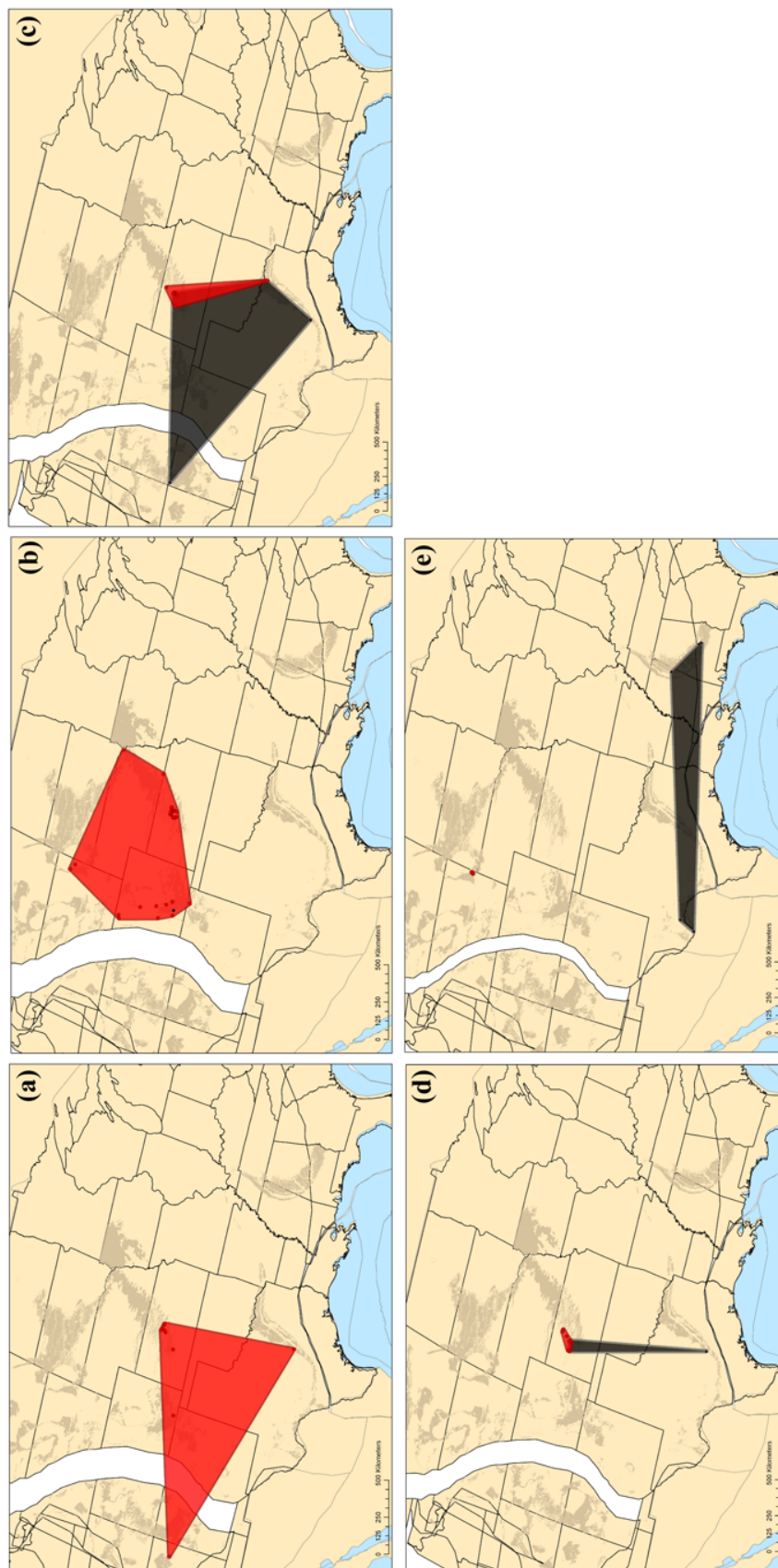
Appendix 1-15. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Squalicorax falcatus* (red) and *Tylosaurus* sp. (blue) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



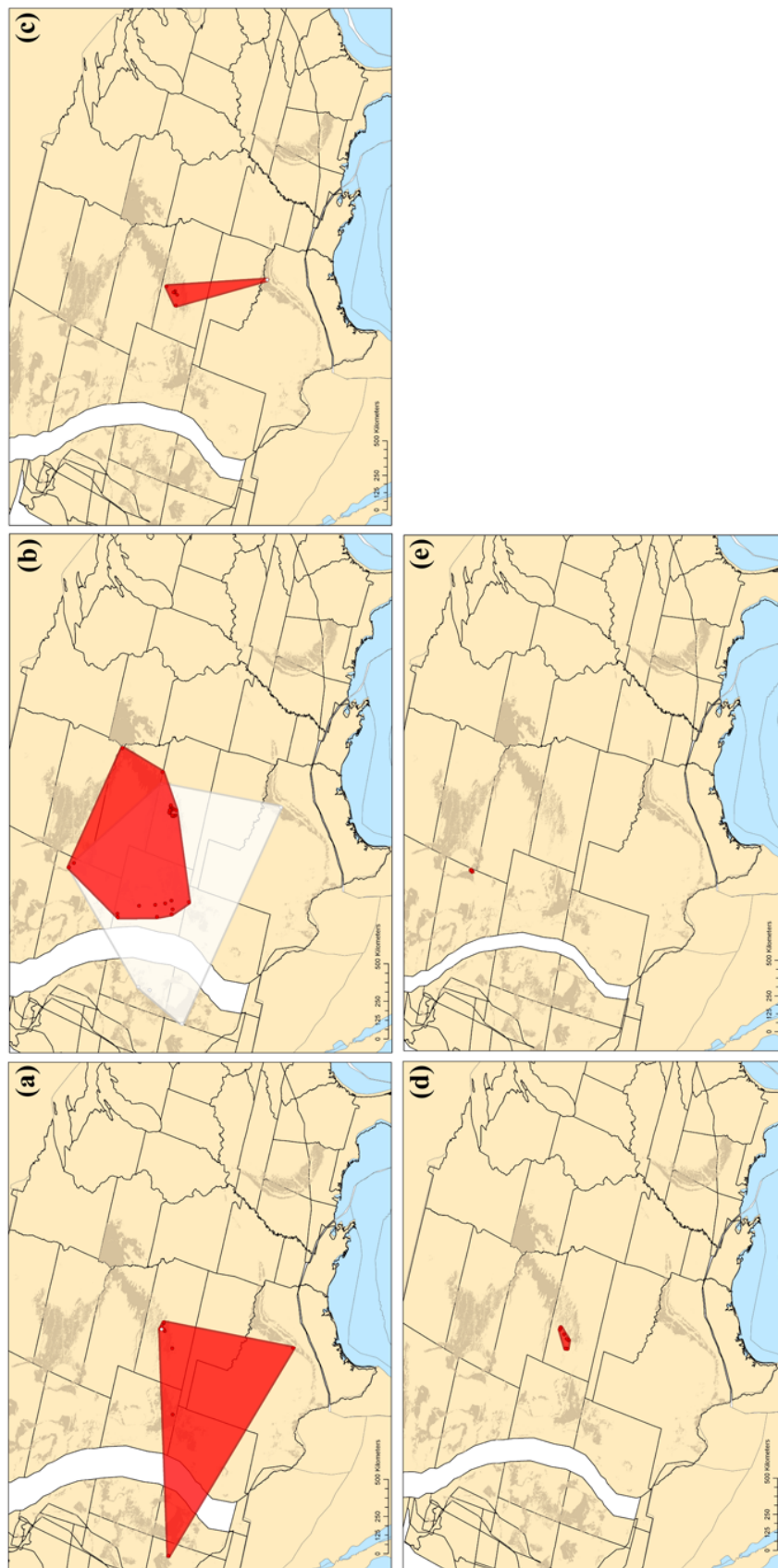
Appendix 1-16. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Squalicorax falcatus* (red) and *Xiphactinus* sp. (pink) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



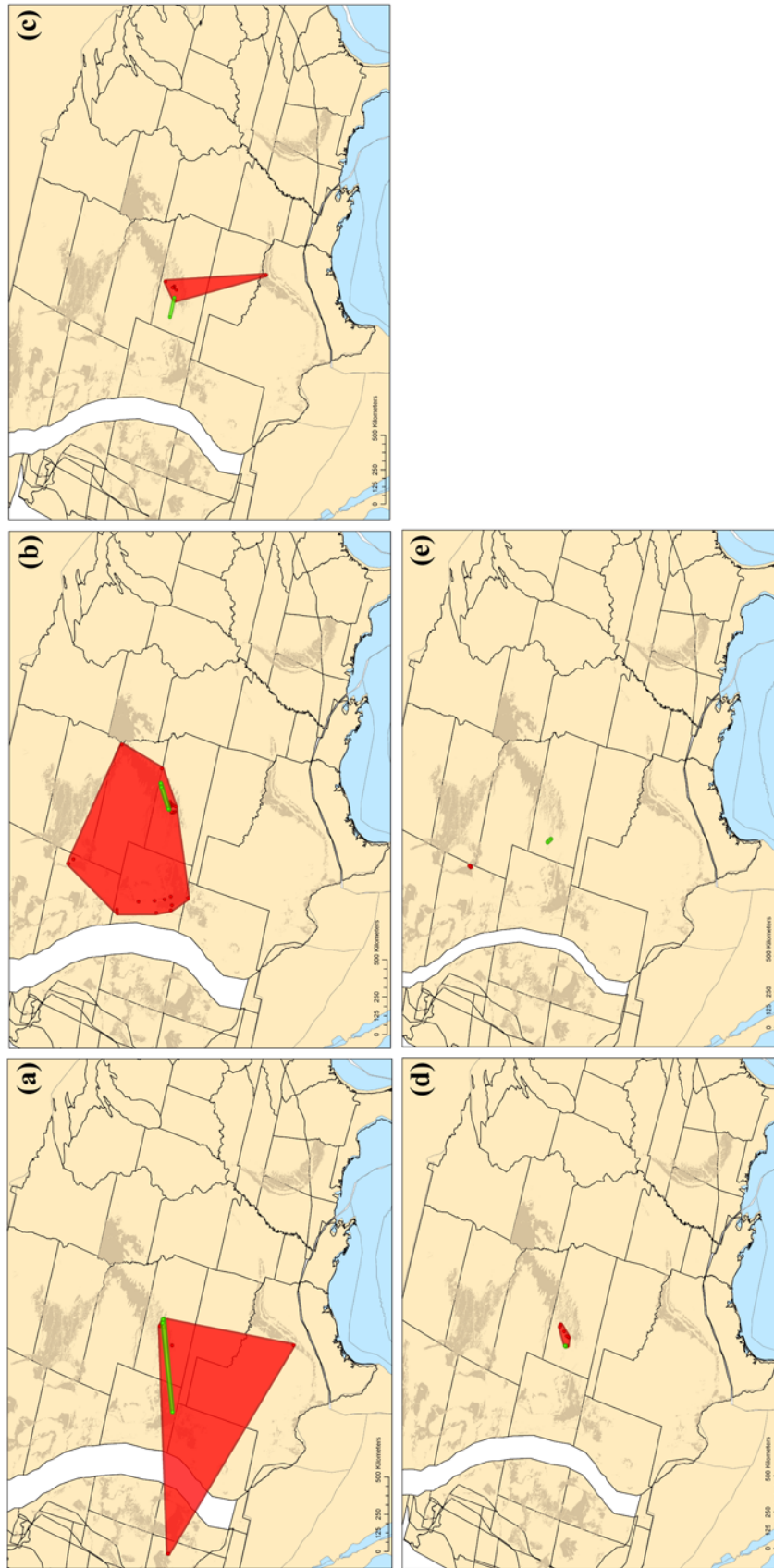
Appendix 1-17. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Squalicorax falcatus* (red) and *Ptychodus anonymous* (grey) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



Appendix 1-18. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Squalicorax falcatus* (red) and *Ptychodus mortoni* (black) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



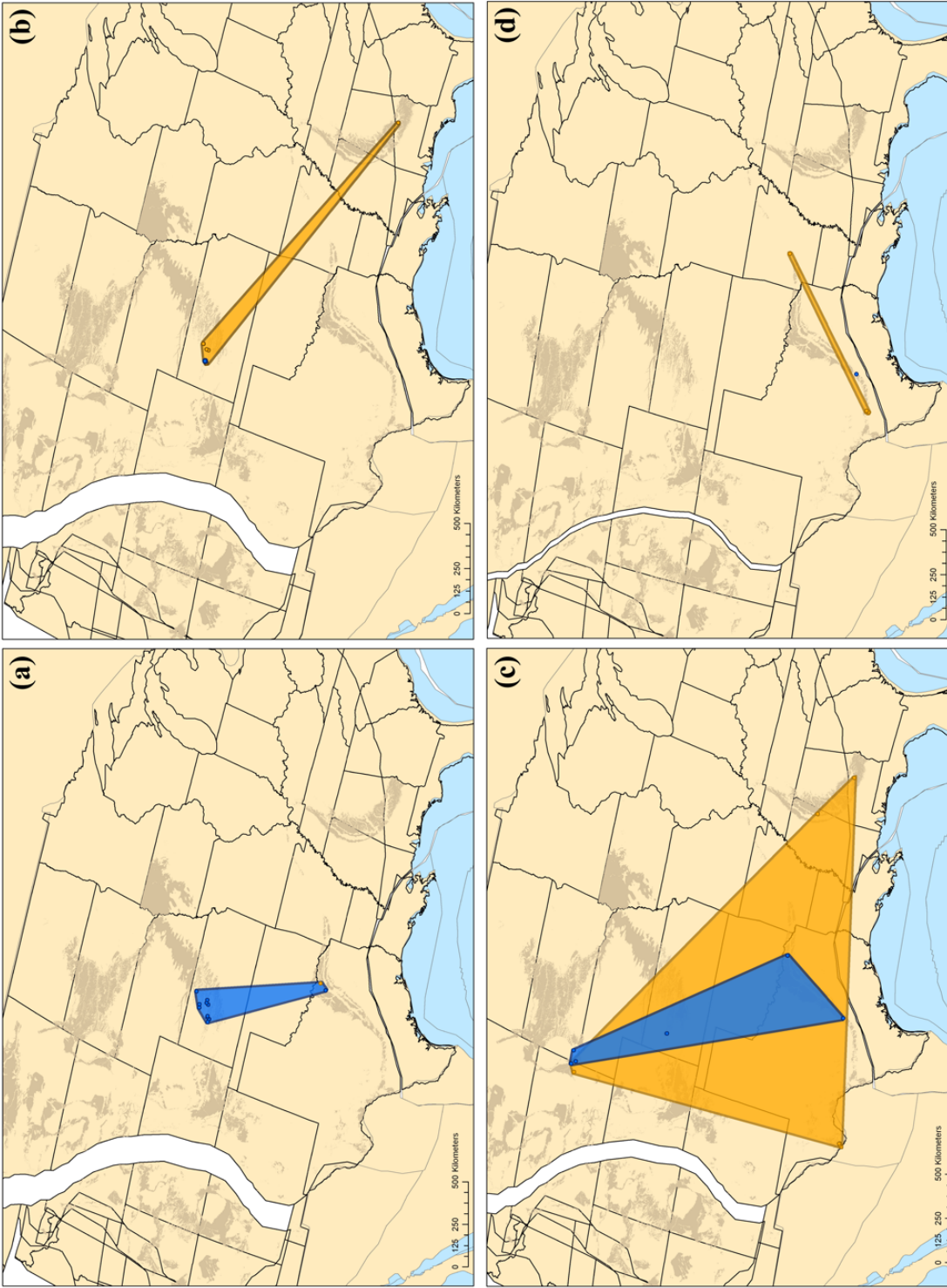
Appendix 1-19. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Squalicorax falcatus* (red) and *Ptychodus whipplei* (white) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



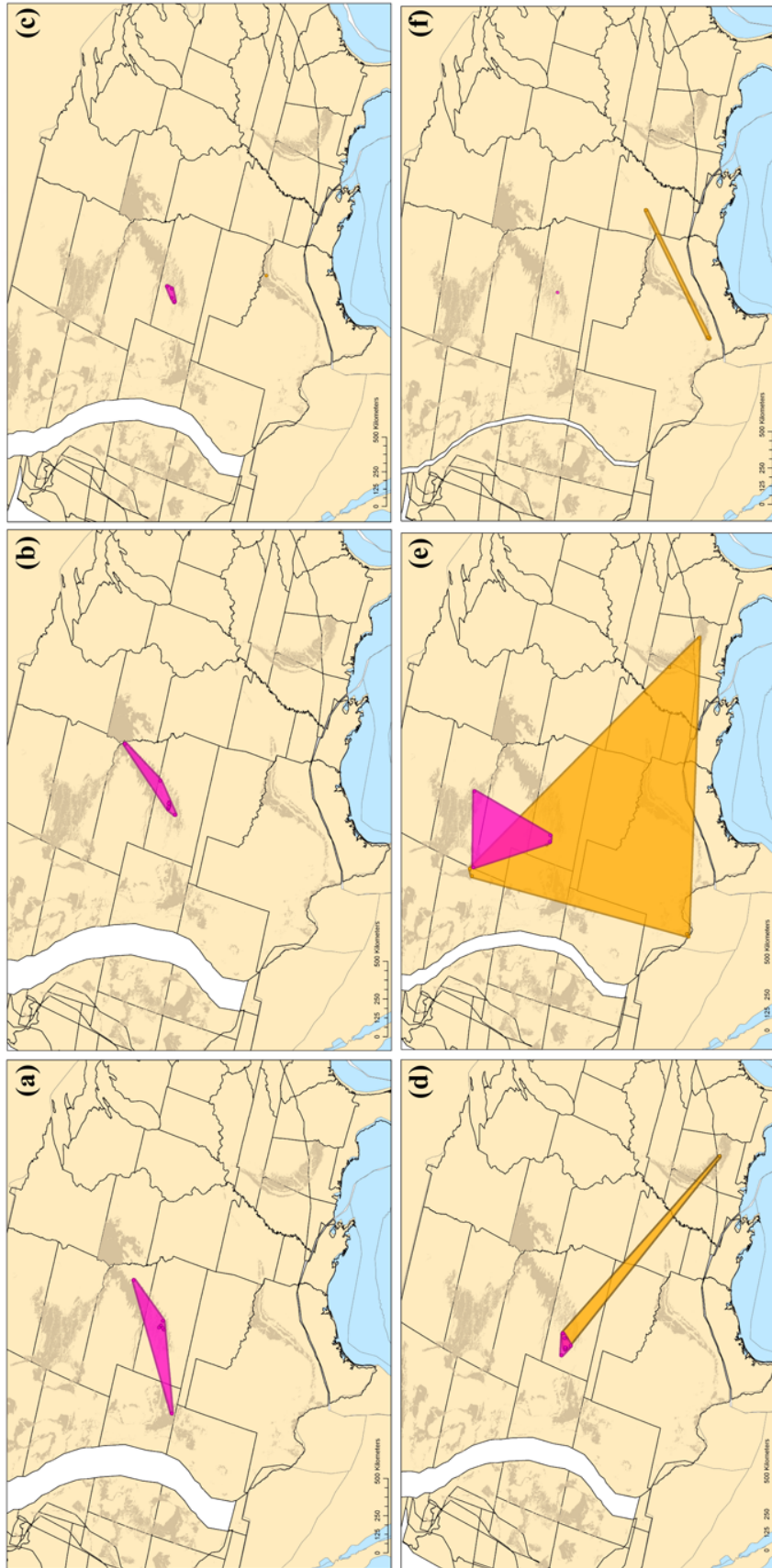
Appendix 1-20. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Squalicorax falcatus* (red) and *Rhinobatos incertus* (light green) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



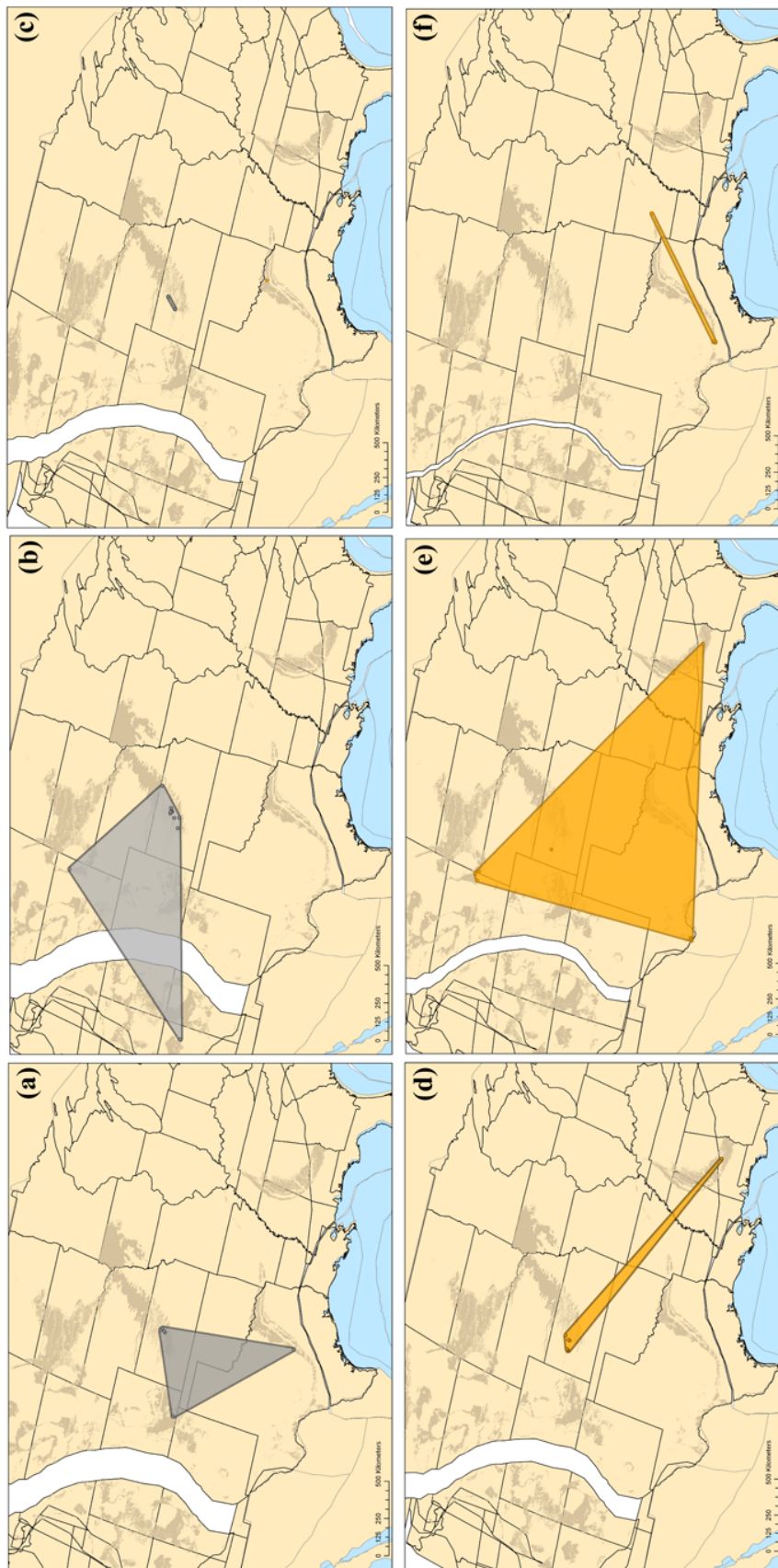
Appendix 1-21. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Squalicorax kaupi* (orange) and *Platecarpus* sp. (dark green) during the Late Cretaceous. Late Cretaceous stages: (a) Coniacian, (b) Santonian, (c) Campanian, (d) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



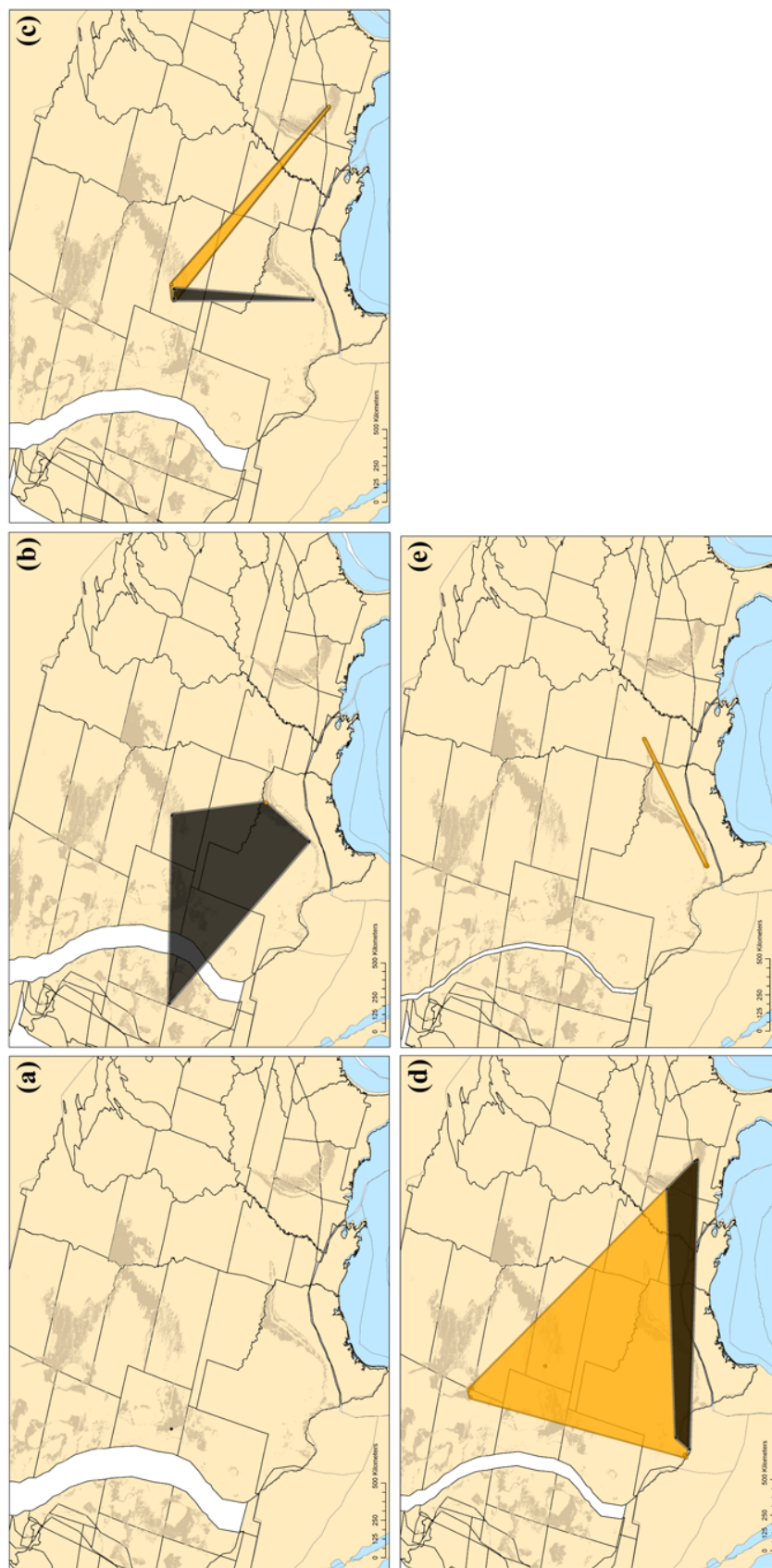
Appendix 1-22. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the paleobiogeographic patterns uncovered for *Squalicorax kaupi* (orange) and *Tylosaurus* sp. (blue) during the Late Cretaceous. Late Cretaceous stages: (a) Coniacian, (b) Santonian, (c) Campanian, (d) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



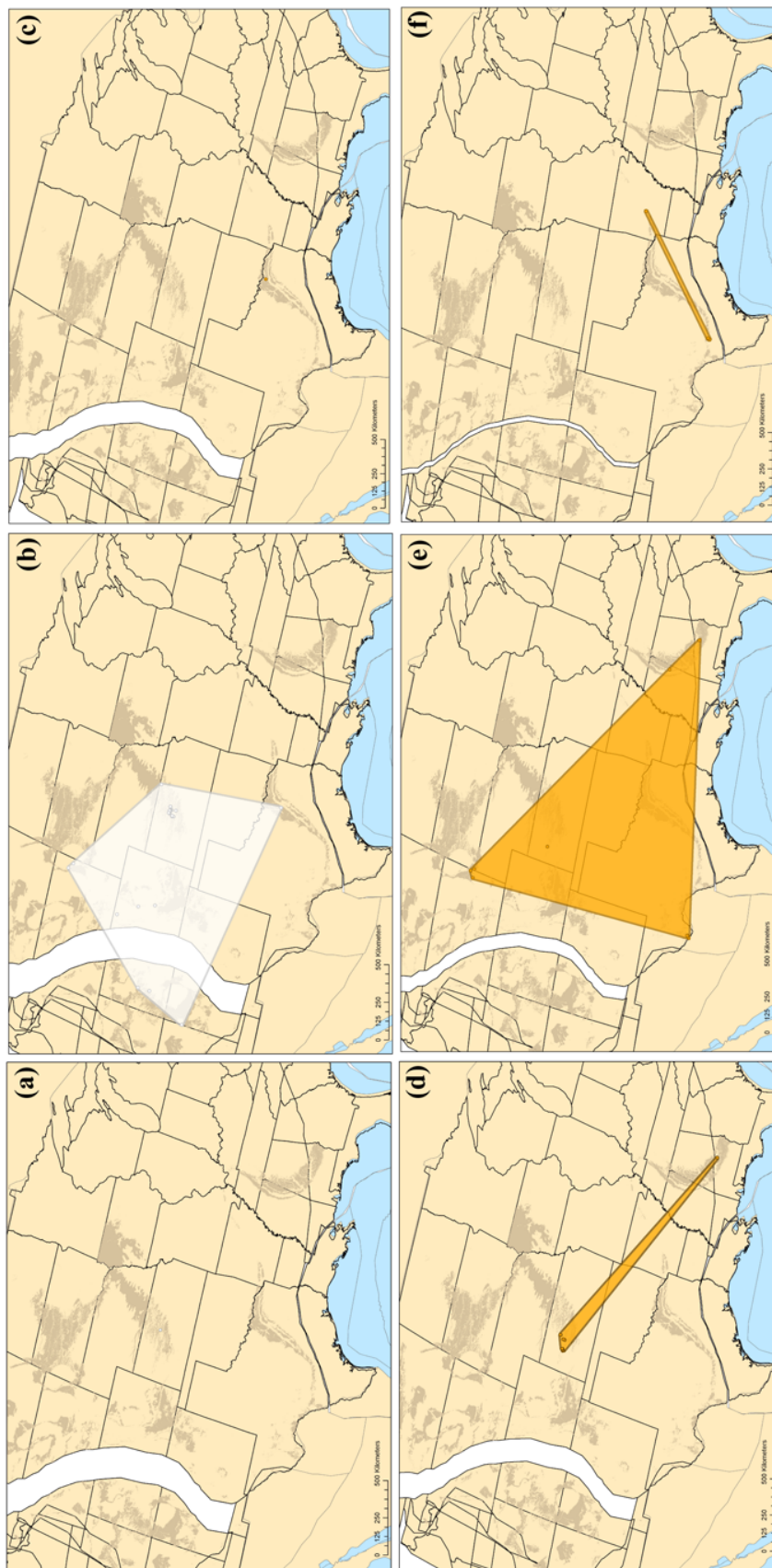
Appendix 1-23. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the paleobiogeographic patterns uncovered for *Squalicorax kaupi* (orange) and *Xiphactinus* sp. (pink) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



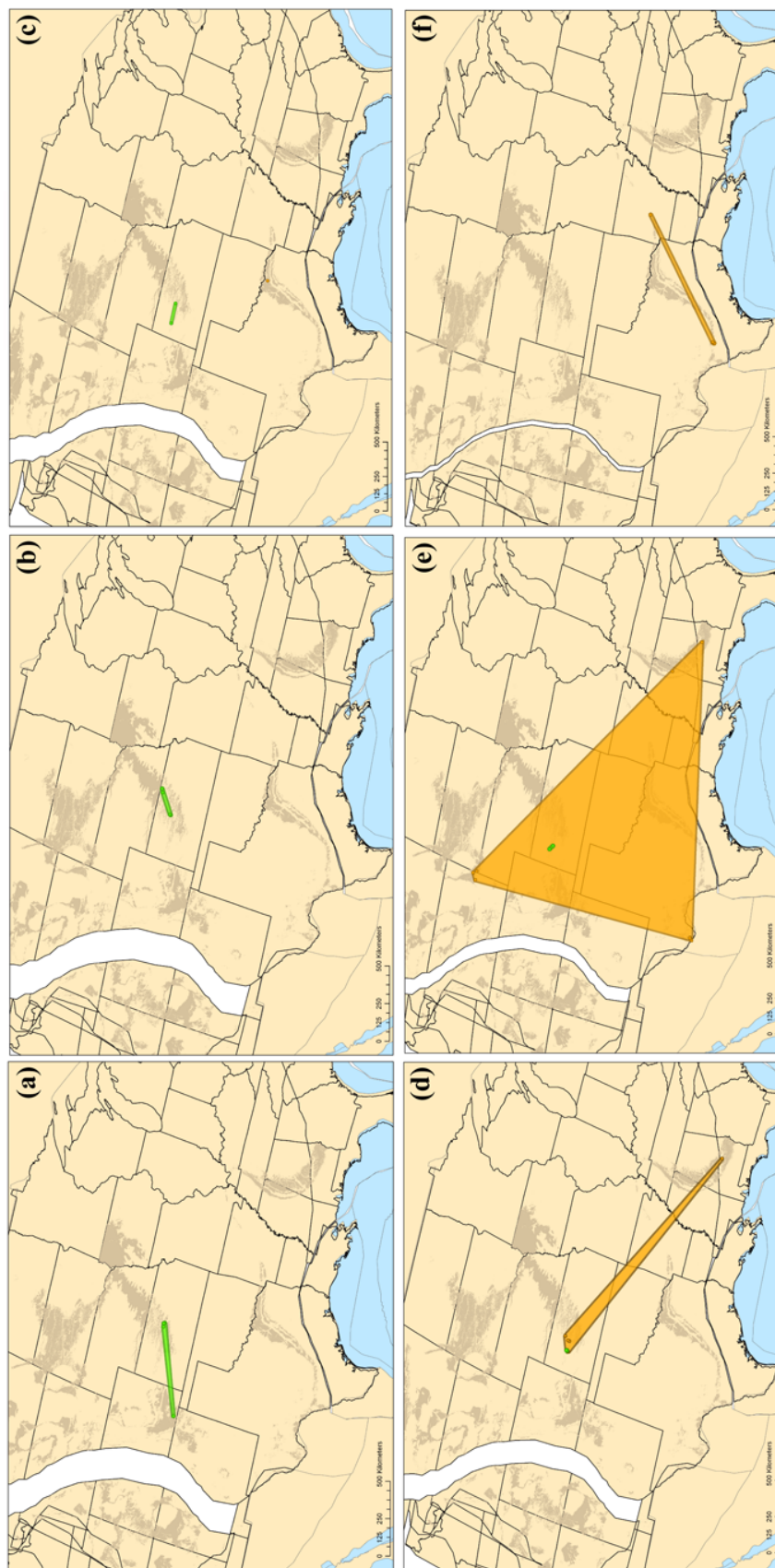
Appendix 1-24. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the paleobiogeographic patterns uncovered for *Squalicorax kaupi* (orange) and *Ptychodus anonymus* (grey) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

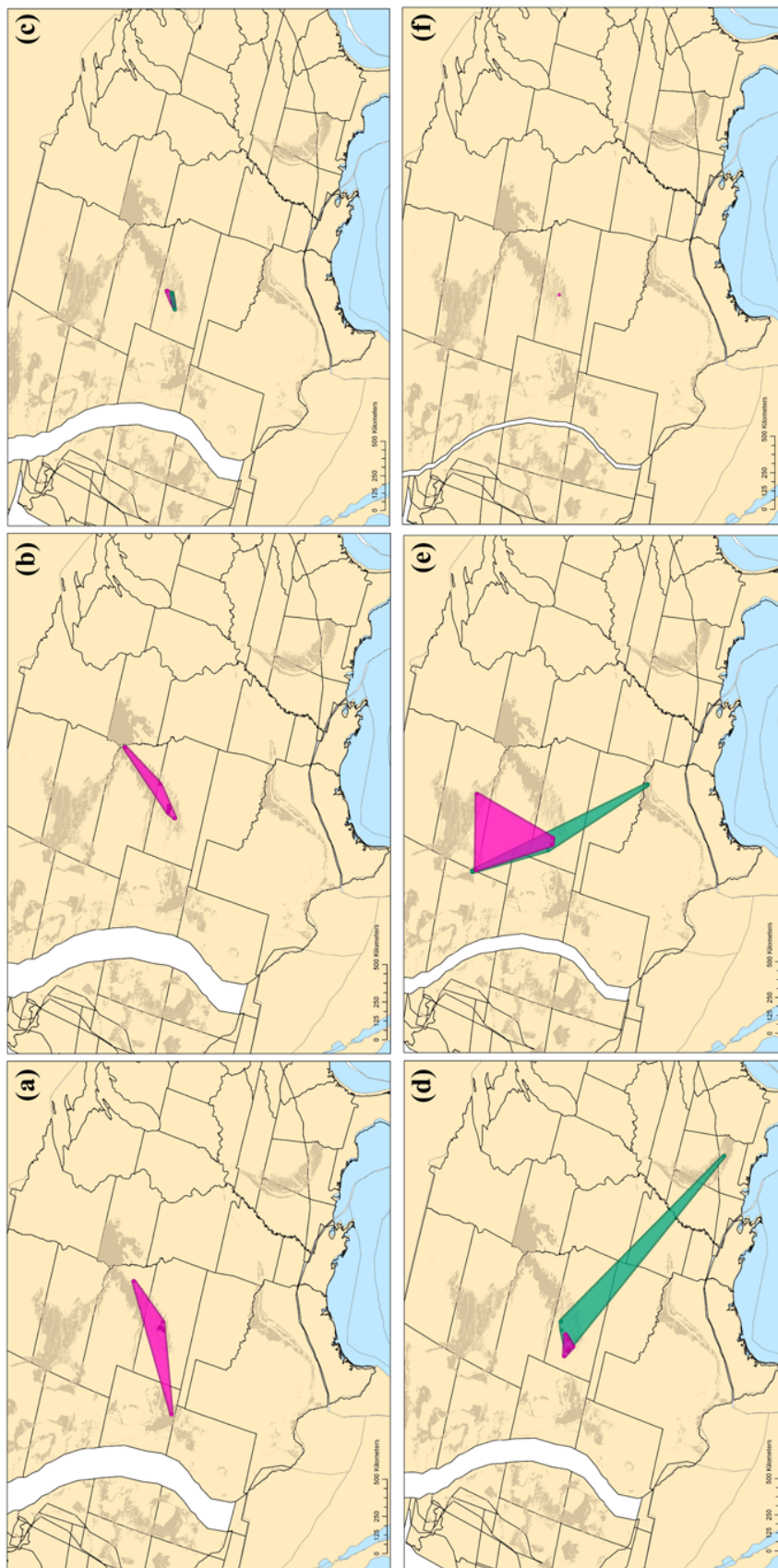


Appendix 1-25. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Squalicorax kaupi* (orange) and *Ptychodus mortoni* (black) during the Late Cretaceous. Late Cretaceous stages: (a) Turonian, (b) Coniacian, (c) Santonian, (d) Campanian, (e) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

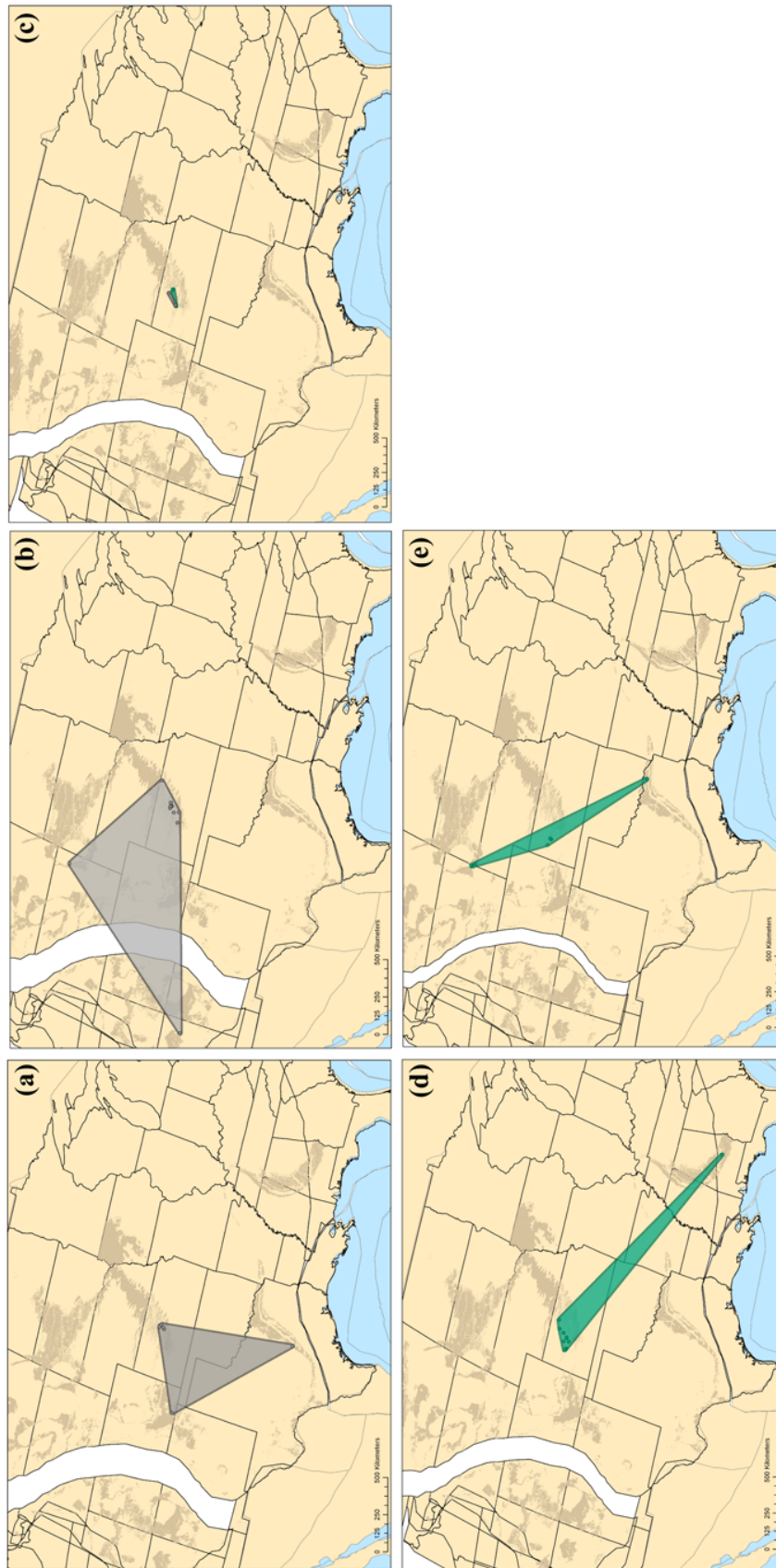


Appendix 1-26. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Squalicorax kaupi* (orange) and *Ptychodus whipplei* (white) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).

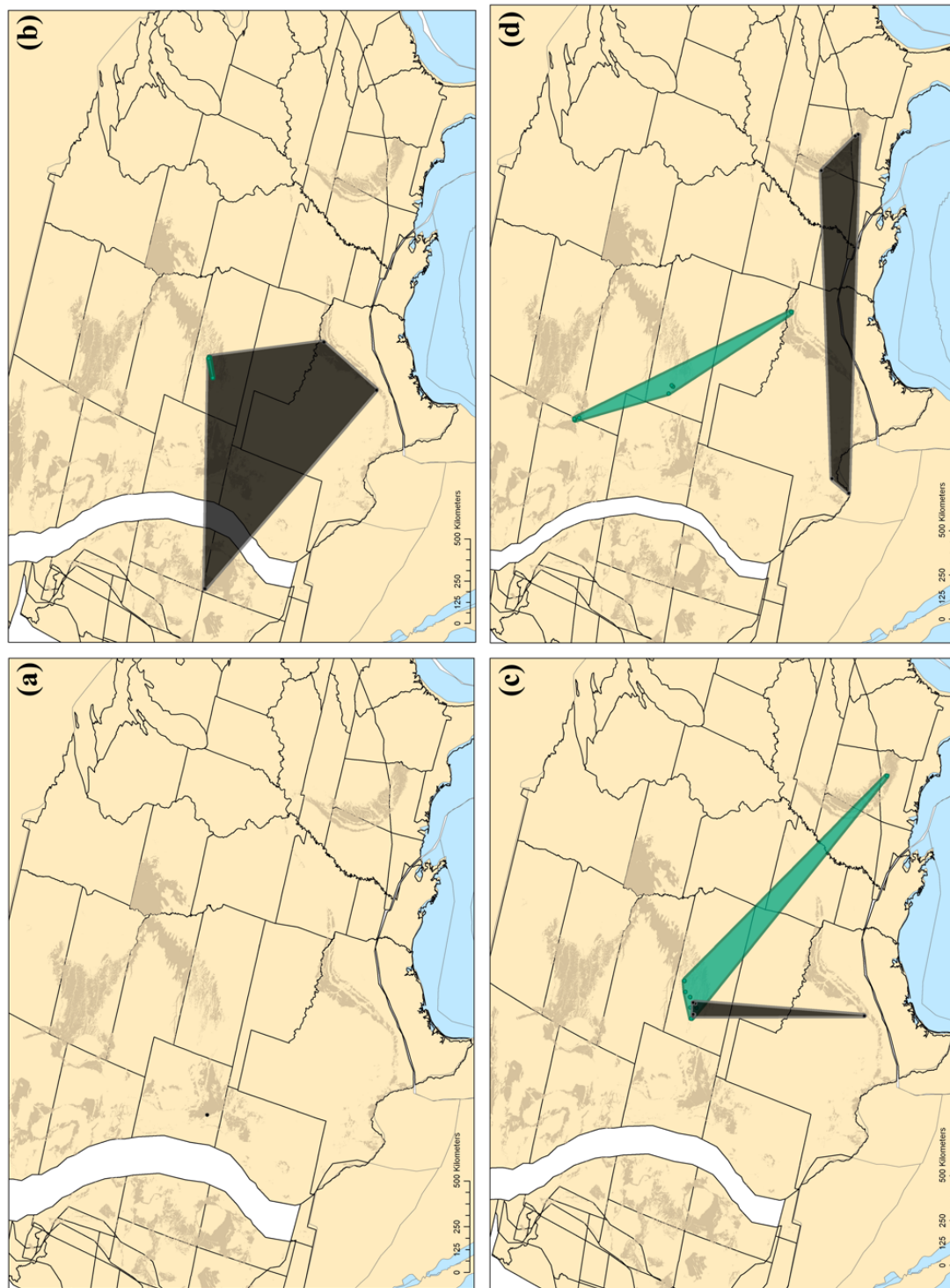




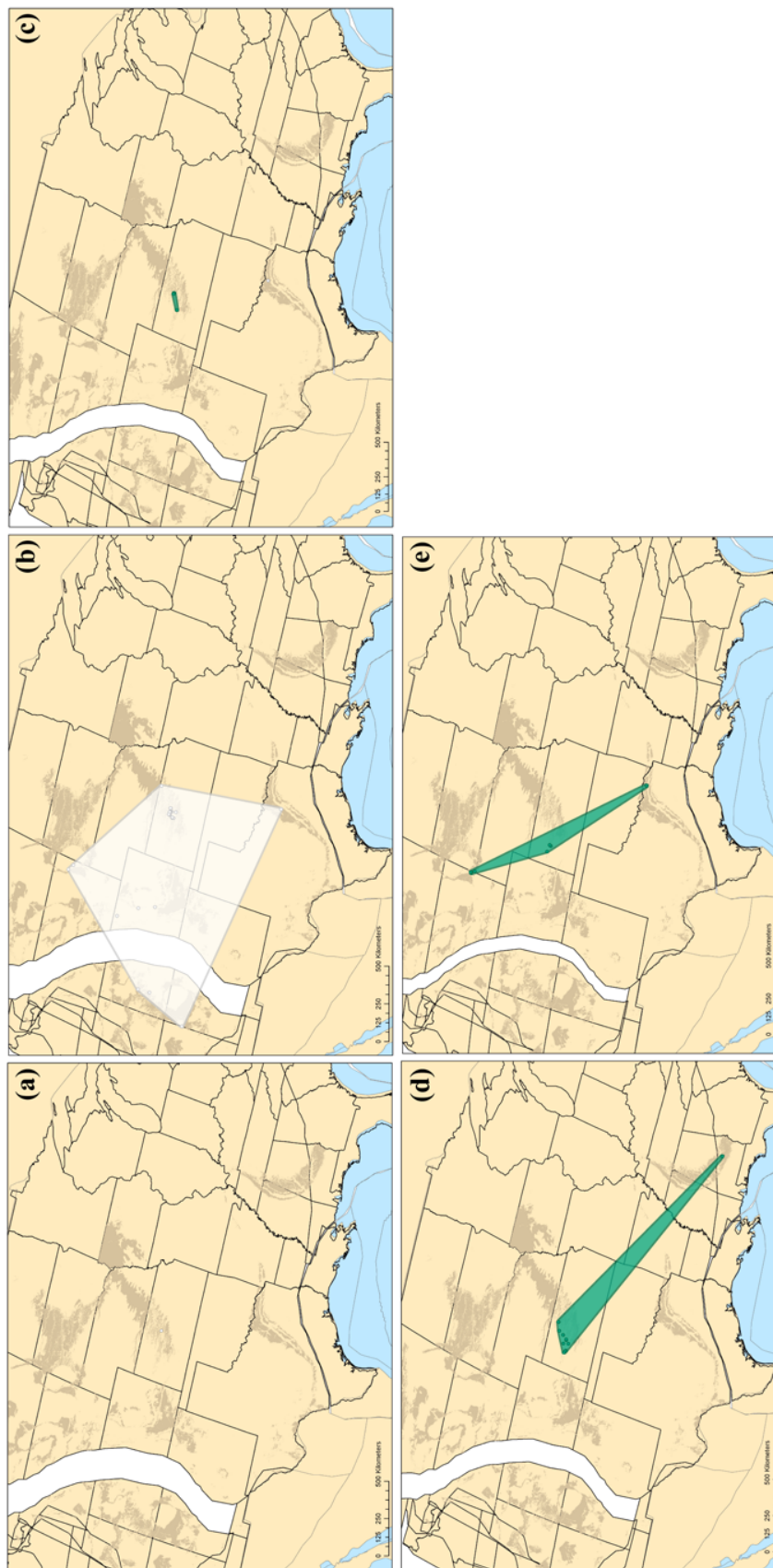
Appendix 1-28. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the paleobiogeographic patterns uncovered for *Plateacarpus* sp. (dark green) and *Xiphactinus* sp. (pink) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



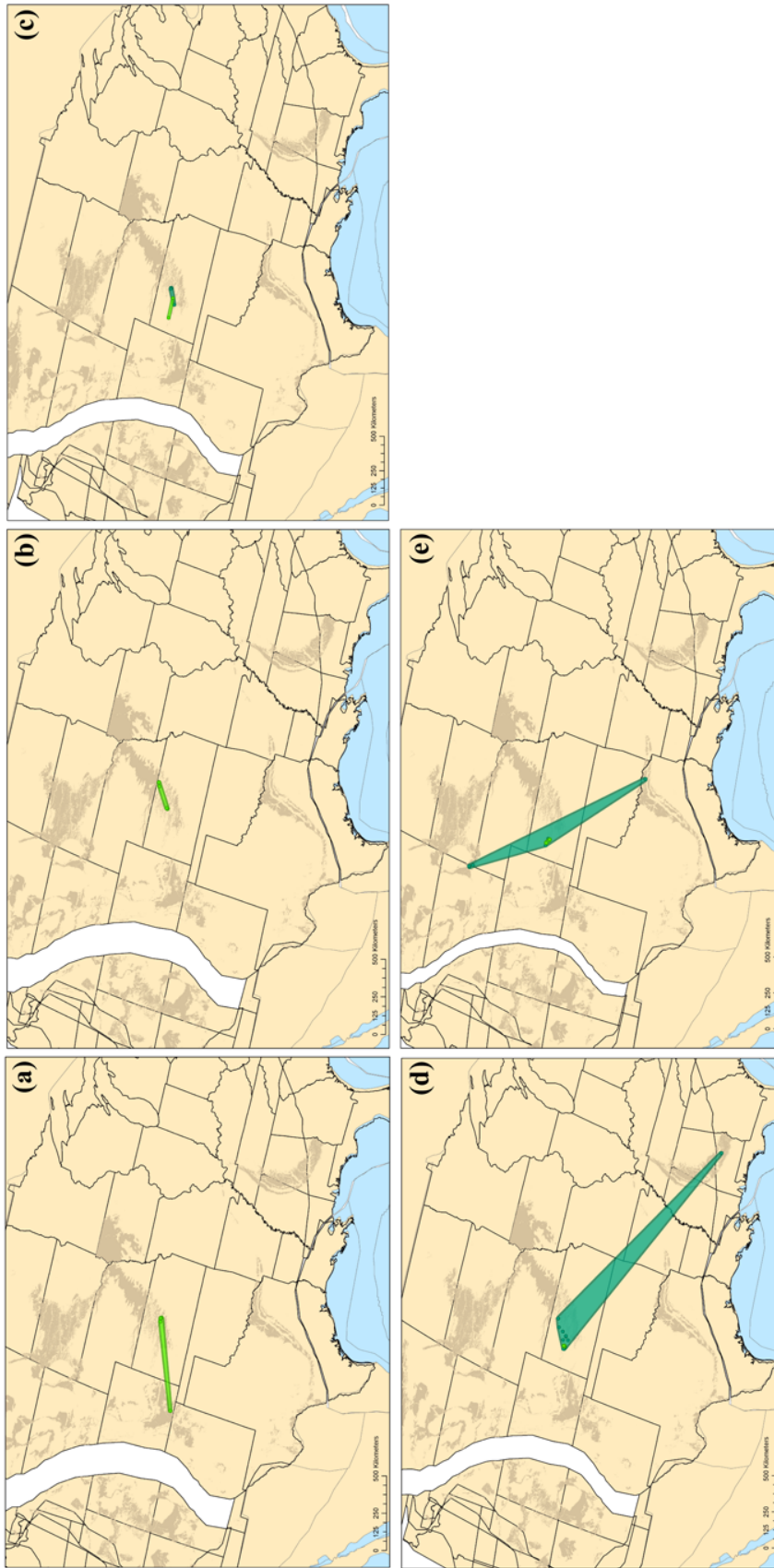
Appendix 1-29. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Plateacarpus* sp. (dark green) and *Ptychodus anomymus* (grey) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



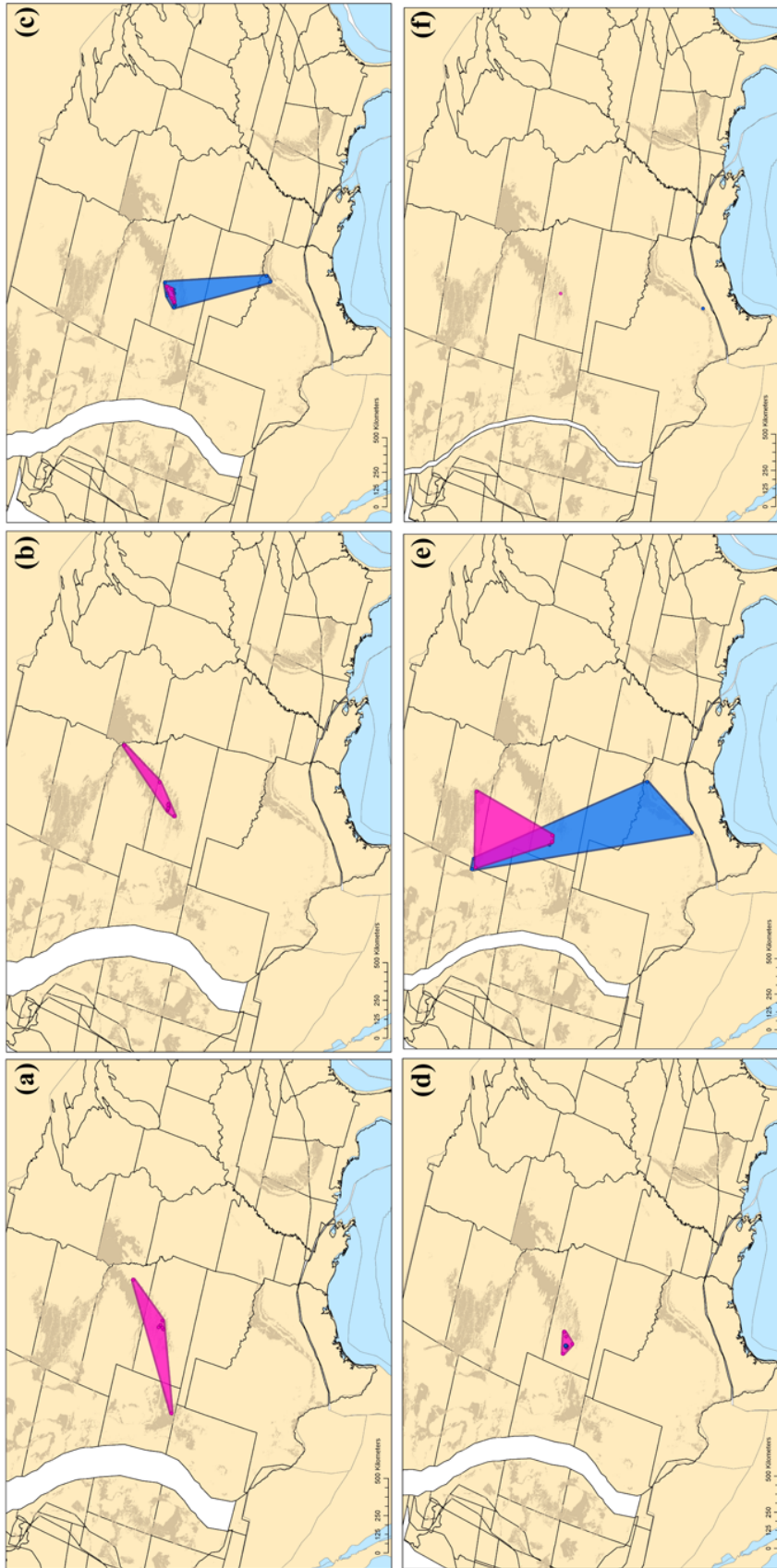
Appendix 1-30. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Plateotectonites* sp. (dark green) and *Pseudoschisma mormoni* (black) during the Late Cretaceous. Late Cretaceous stages: (a) Turonian, (b) Coniacian, (c) Santonian, (d) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



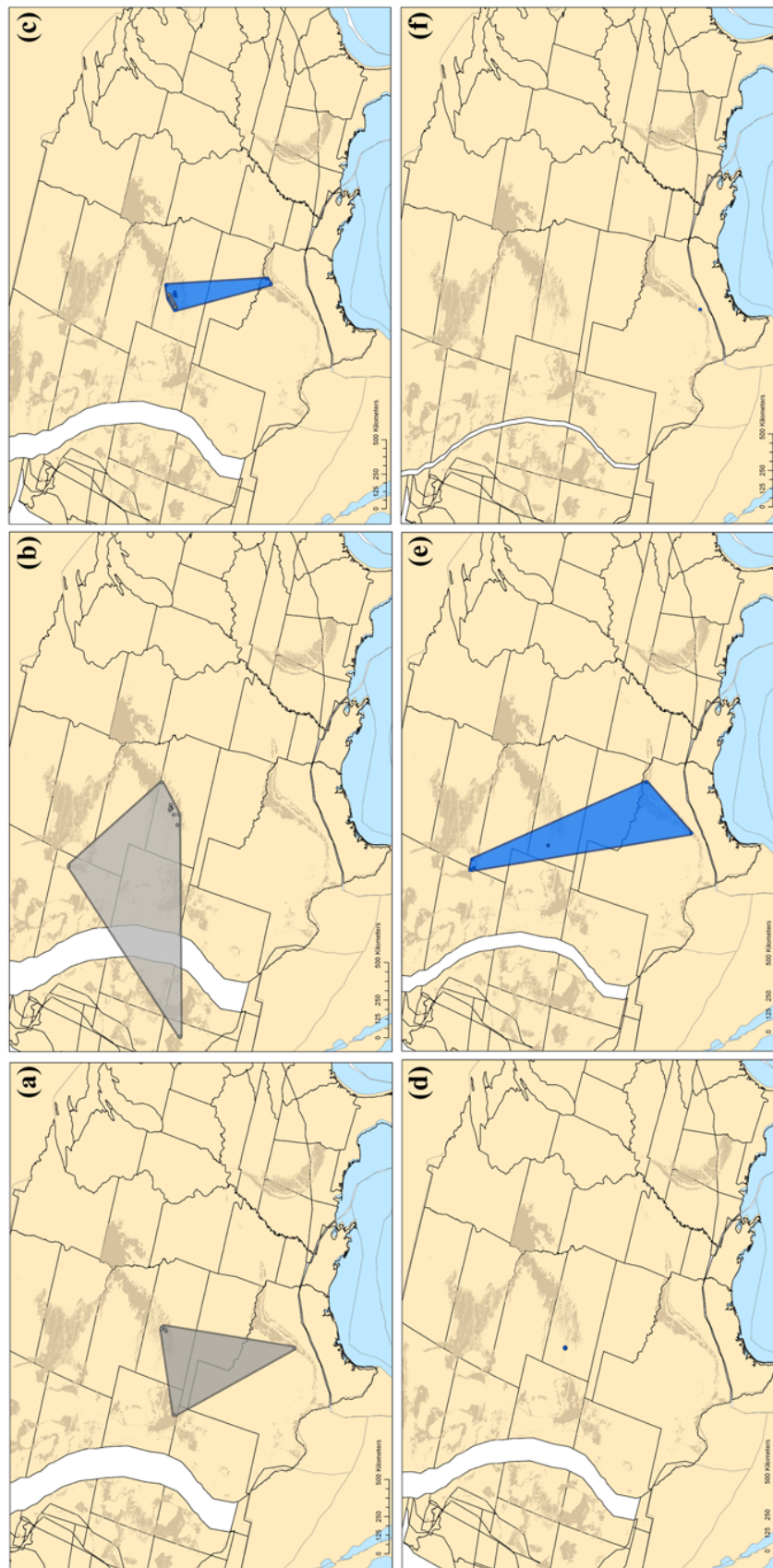
Appendix 1-31. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Plateacarpus* sp. (dark green) and *Ptychodus whipplei* (white) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



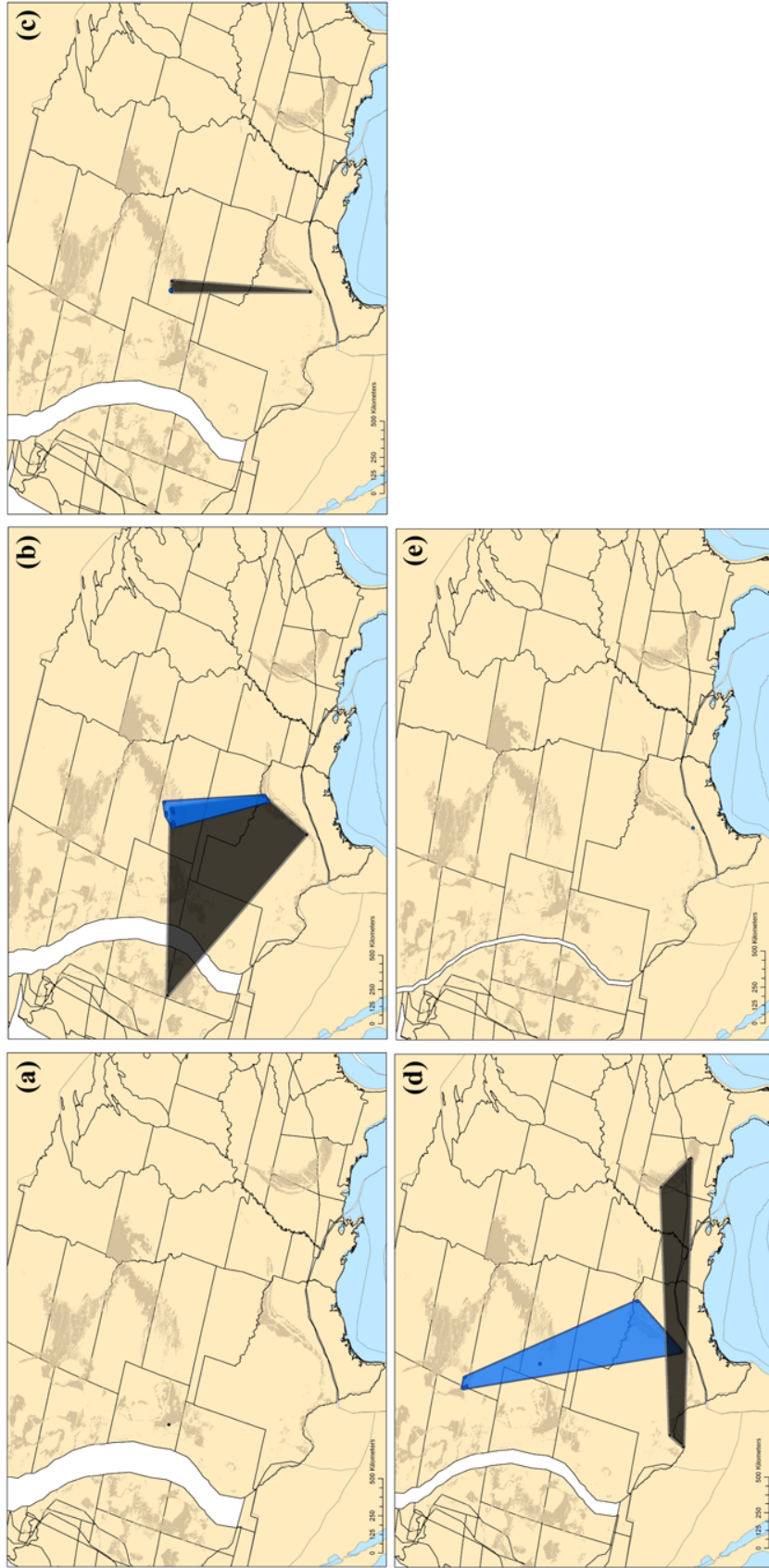
Appendix 1-32. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Plateacarpus* sp. (dark green) and *Rhinobatos incertus* (light green) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



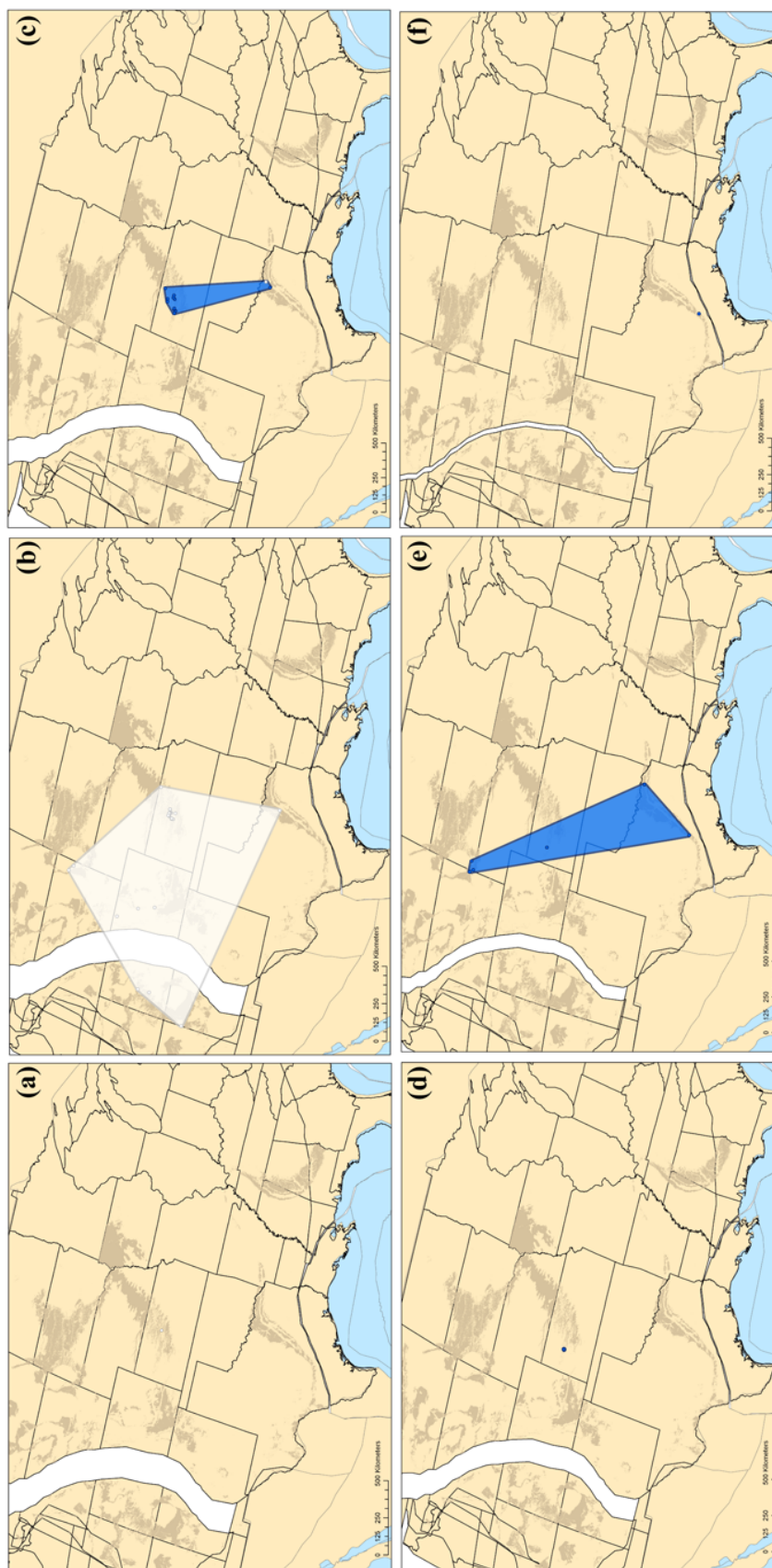
Appendix 1-33. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Tyllosaurus* sp. (blue) and *Xiphactinus* sp. (pink) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



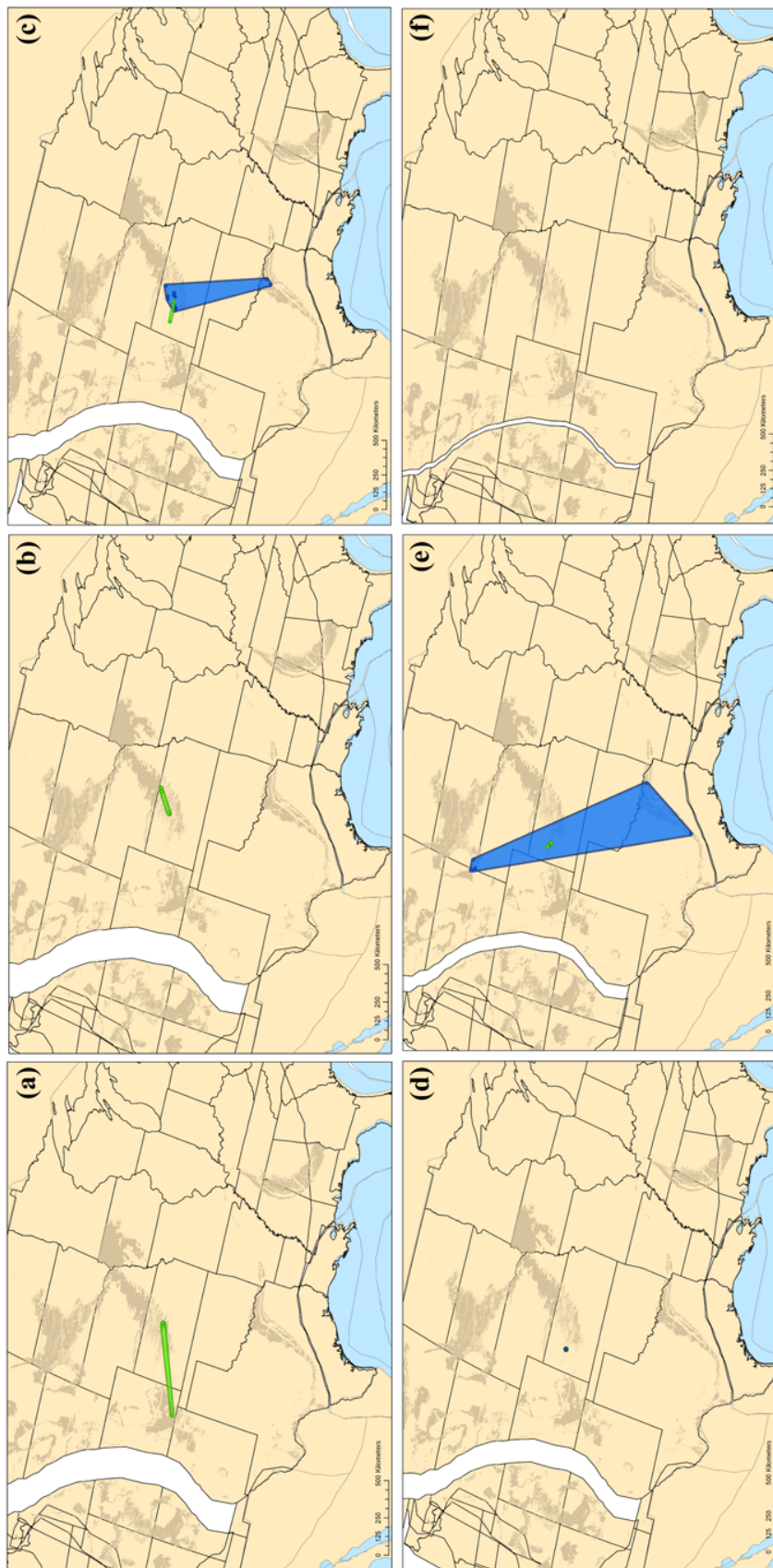
Appendix 1-34. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Tylosaurus* sp. (blue) and *Ptychodus anonymus* (grey) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



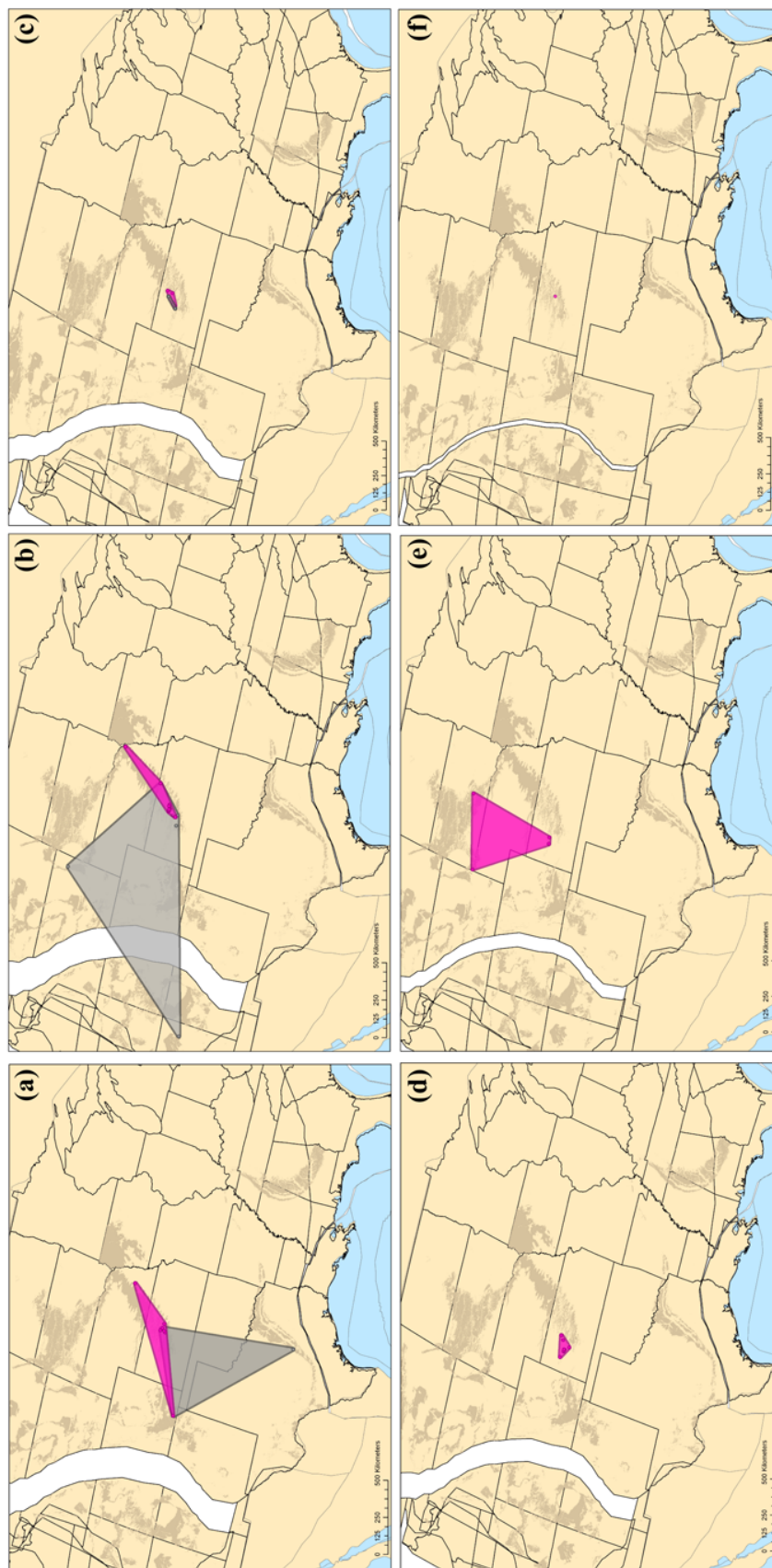
Appendix 1-35. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Tylosaurus* sp. (blue) and *Ptychodus mortoni* (black) during the Late Cretaceous. Late Cretaceous stages: (a) Turonian, (b) Coniacian, (c) Santonian, (d) Campanian, (e) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



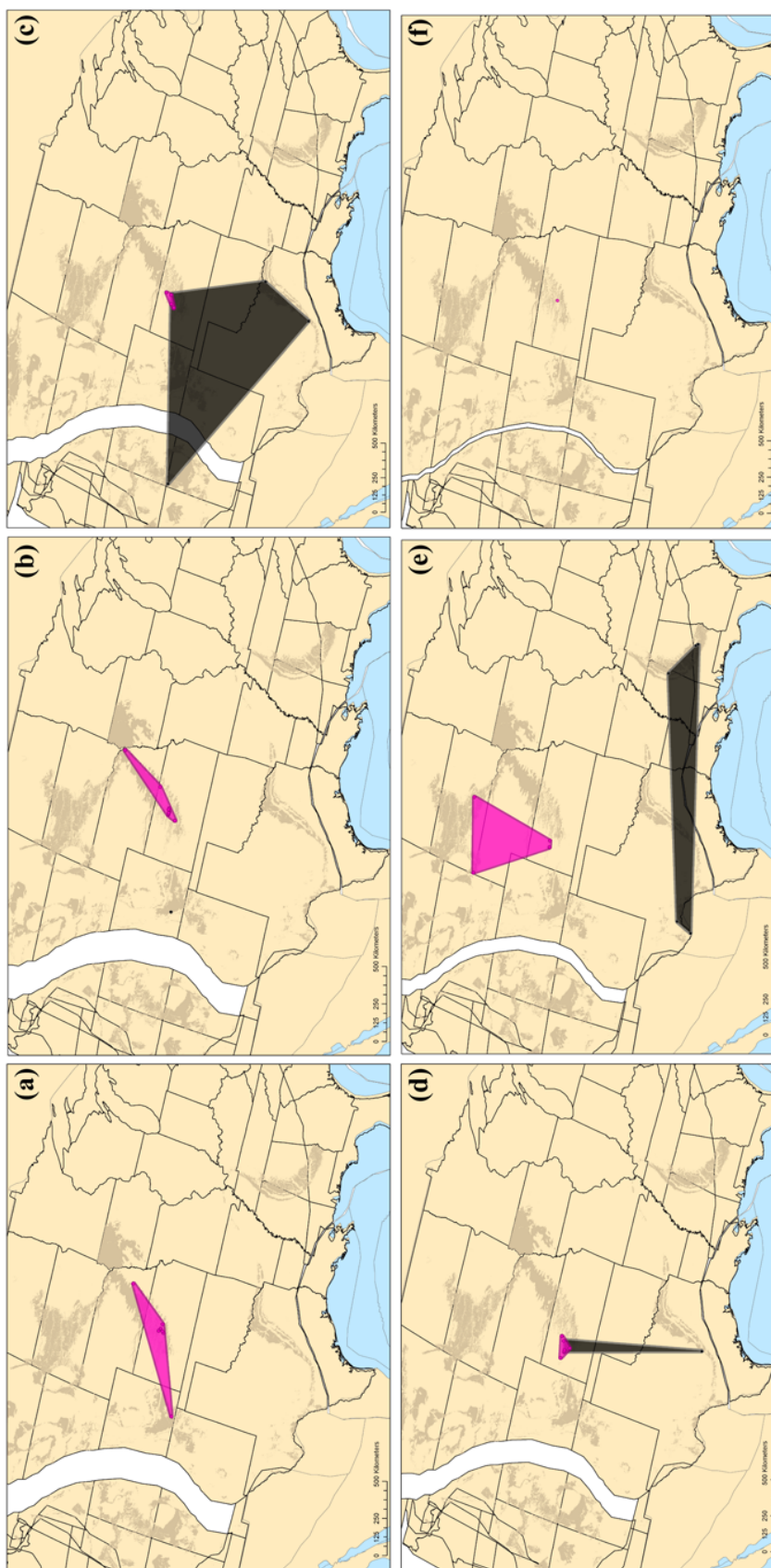
Appendix 1-36. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Tylosaurus* sp. (blue) and *Ptychodus whipplei* (white) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



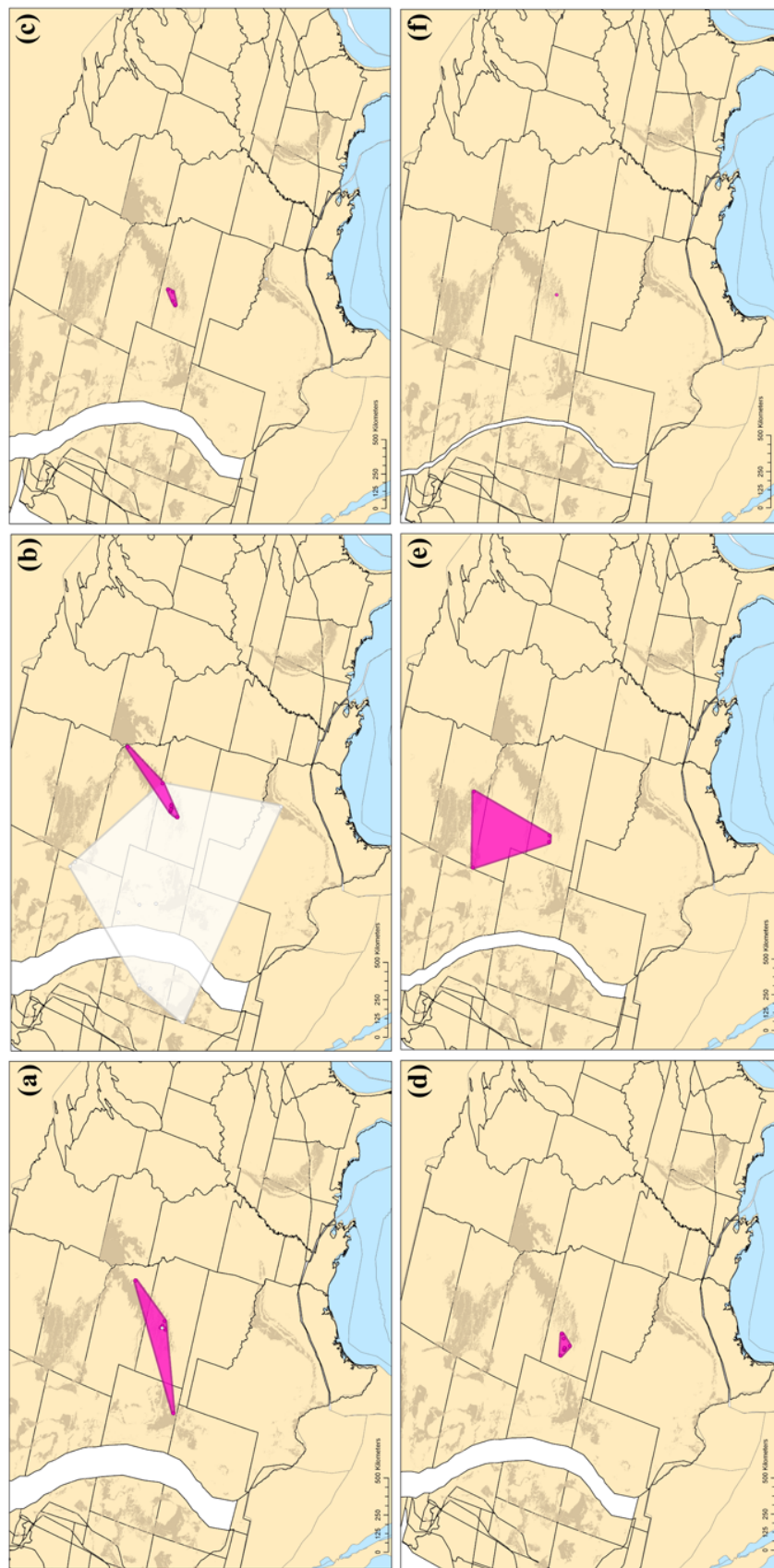
Appendix 1-37. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Tylosaurus* sp. (blue) and *Rhinobatos incertus* (light green) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



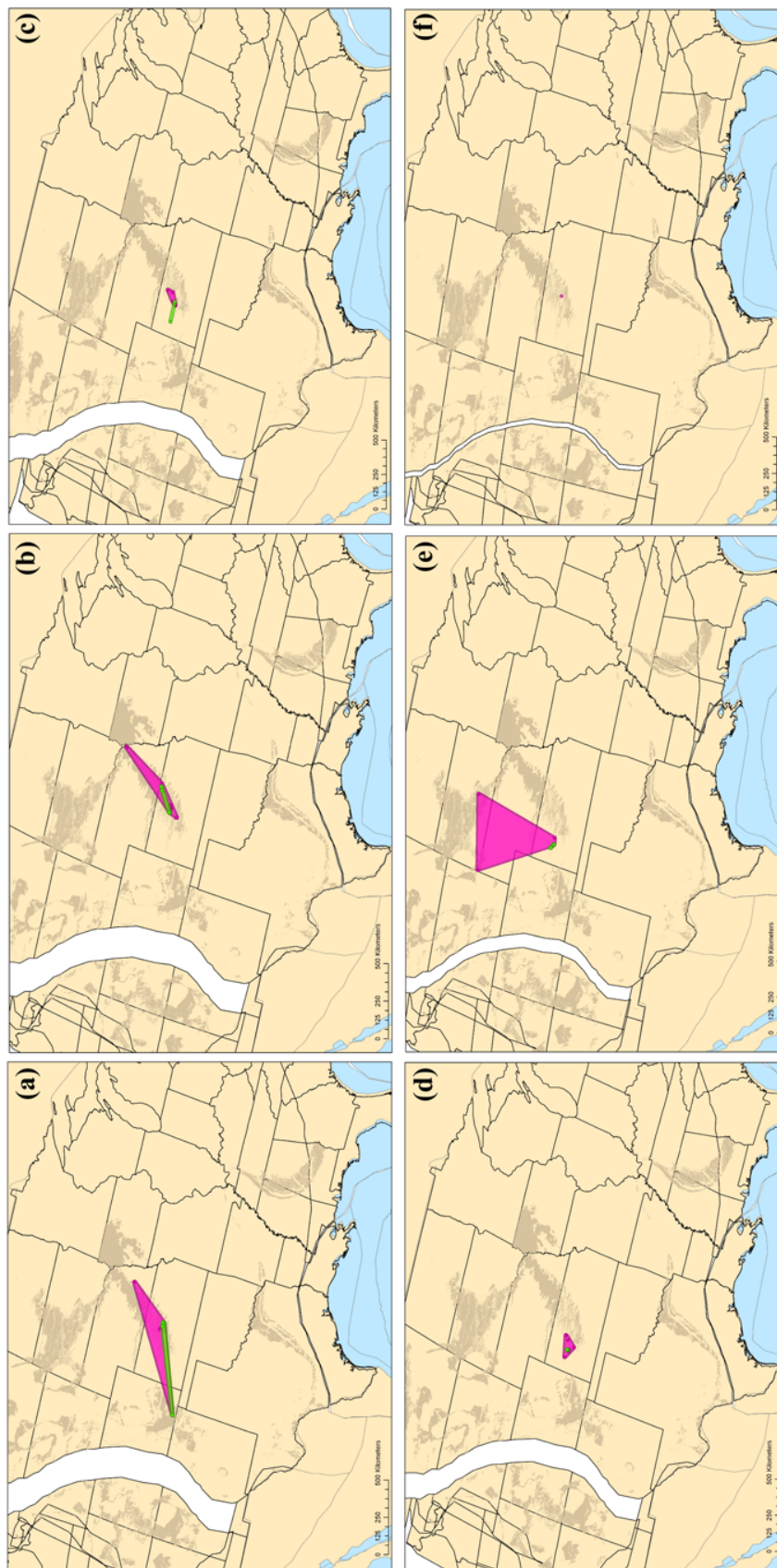
Appedix 1-38. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Xiphactinus* sp. (pink) and *Ptychodus anomymus* (grey) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



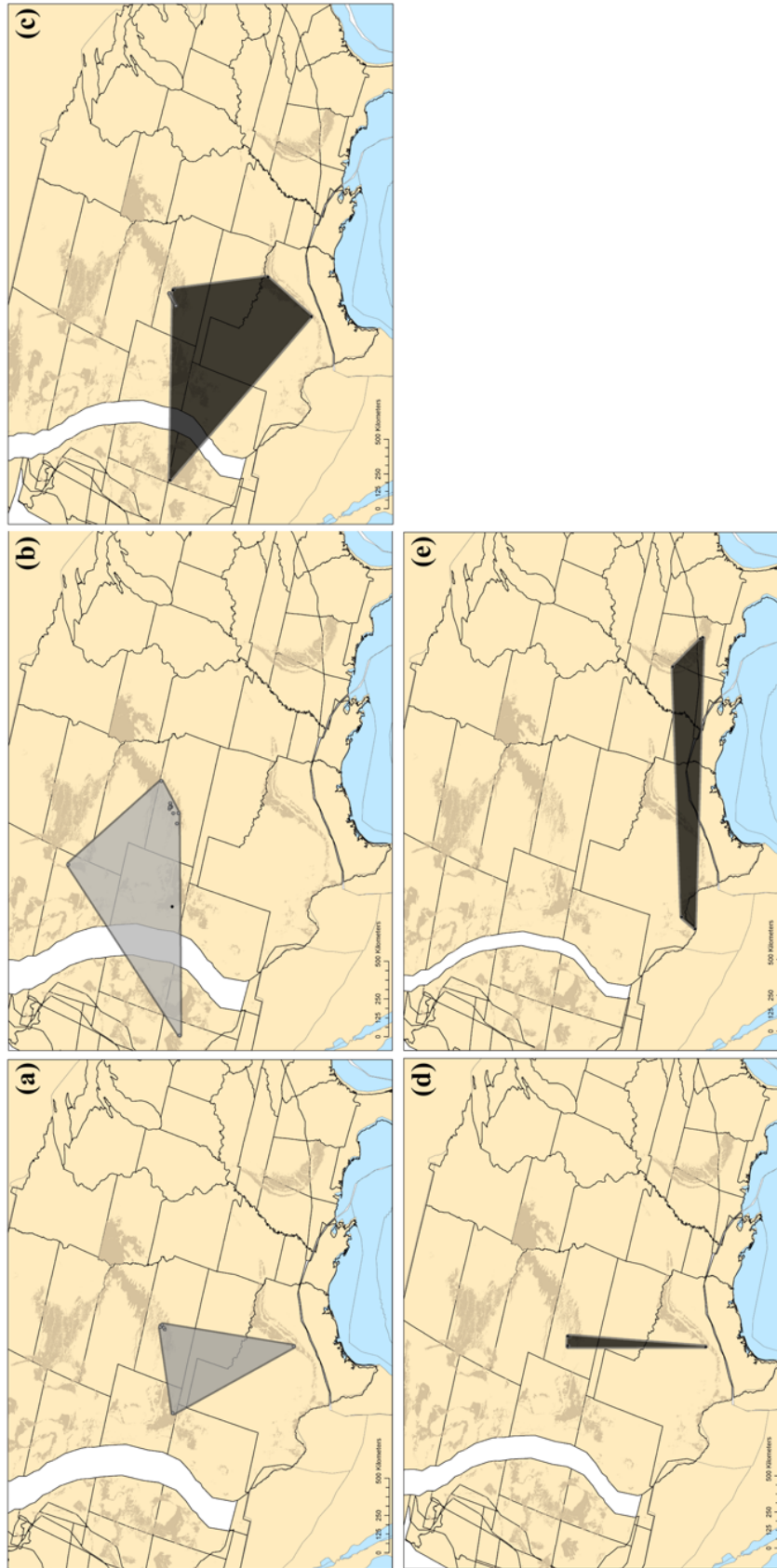
Appendix 1-39. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the paleobiogeographic patterns uncovered for *Xiphactinus* sp. (pink) and *Pseudosuchia mormoni* (black) during the Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



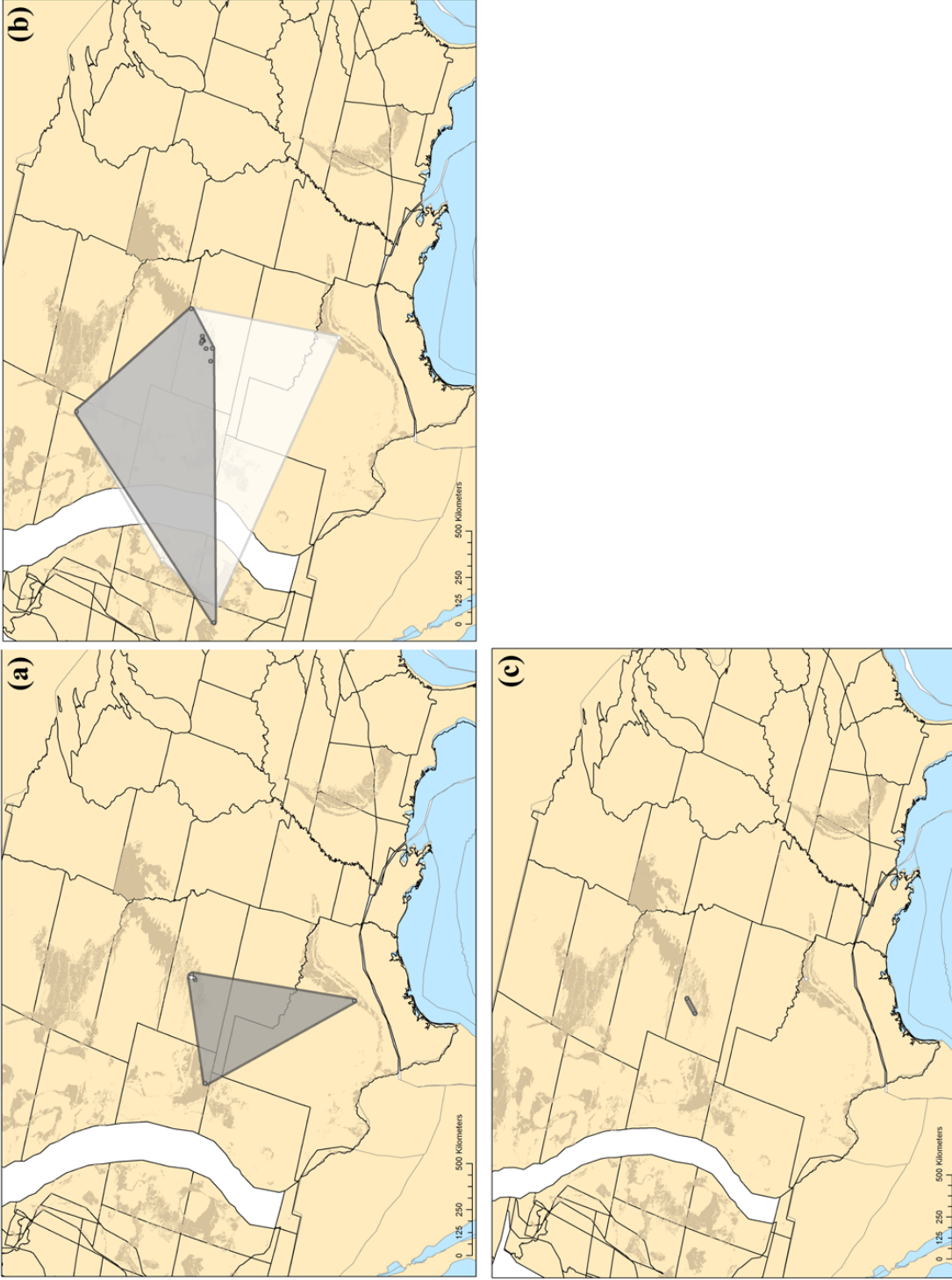
Appendix 1-40. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Xiphactinus* sp. (pink) and *Ptychodus whipplei* (white) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



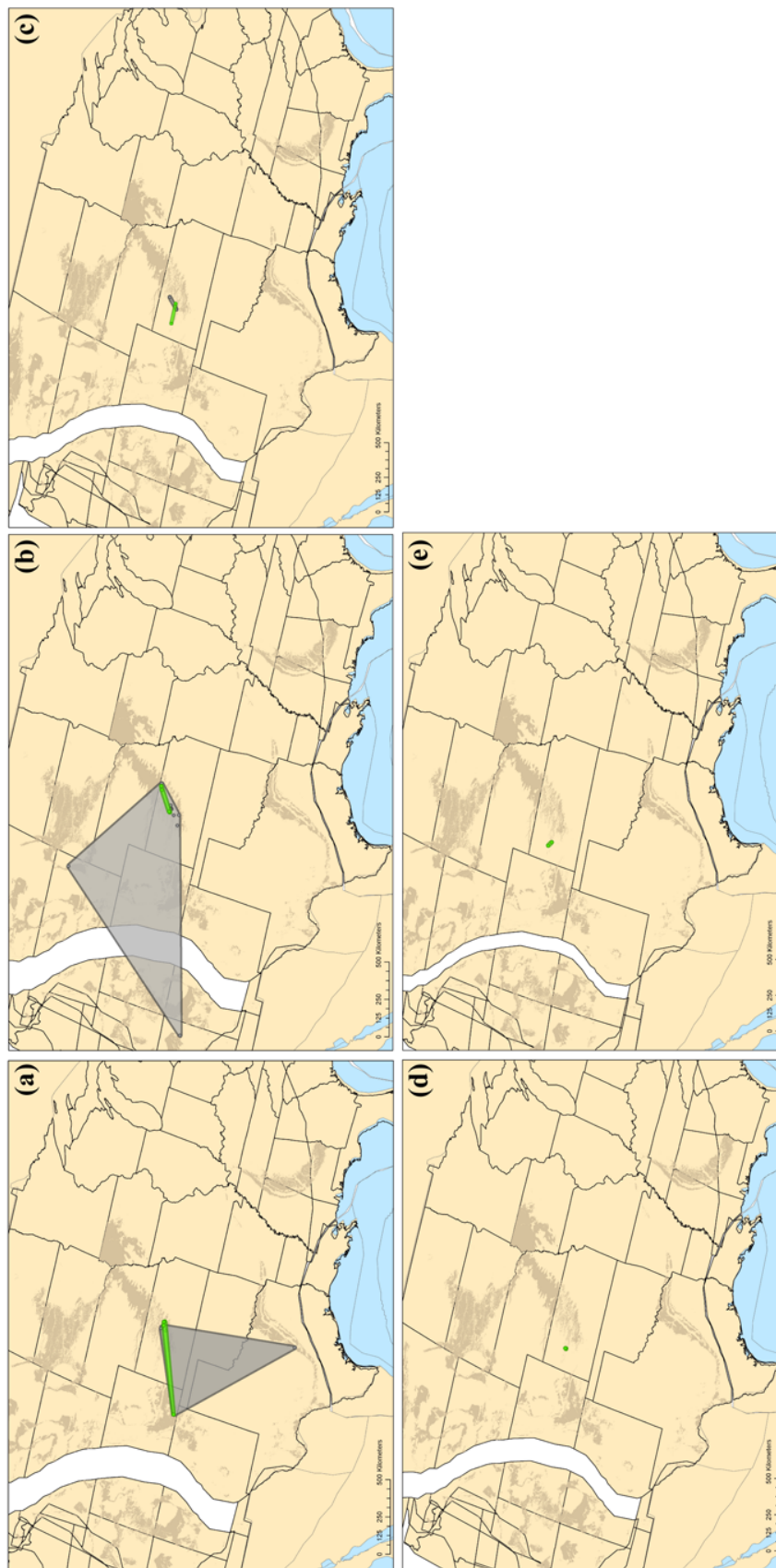
Appendix 1-41. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Xiphactinus* sp. (pink) and *Rhinobatos incertus* (light green) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian, (f) Maastrichtian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



Appendix 1-42. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Psychodus anomymus* (grey) and *Psychodus mortoni* (black) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



Appendix 1-43 PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Psychodus anonymous* (grey) and *Psychodus whipplei* (white) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



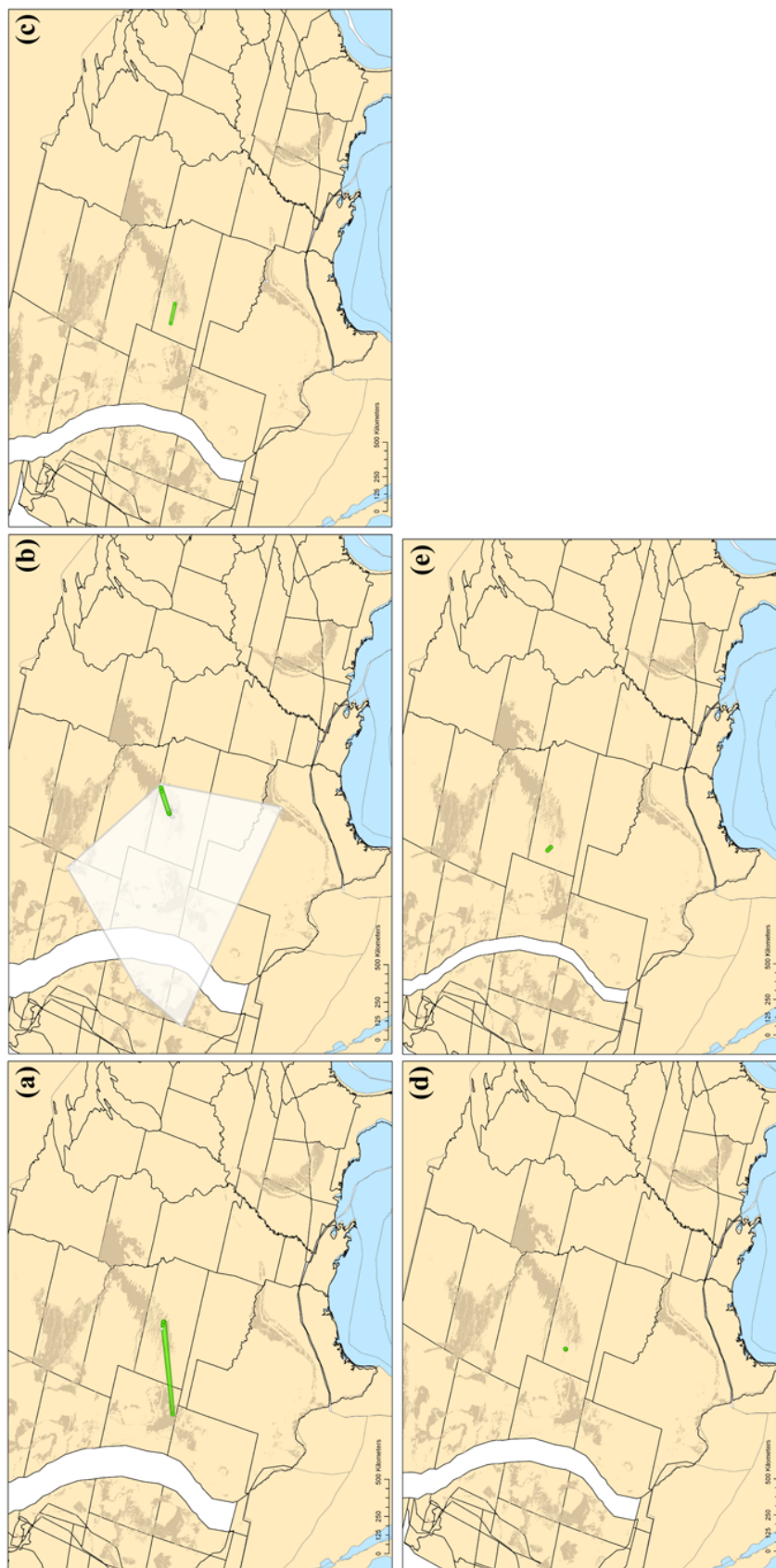
Appendix 1-44. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Pycnodon anomymus* (grey) and *Rhinobatos incertus* (light green) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



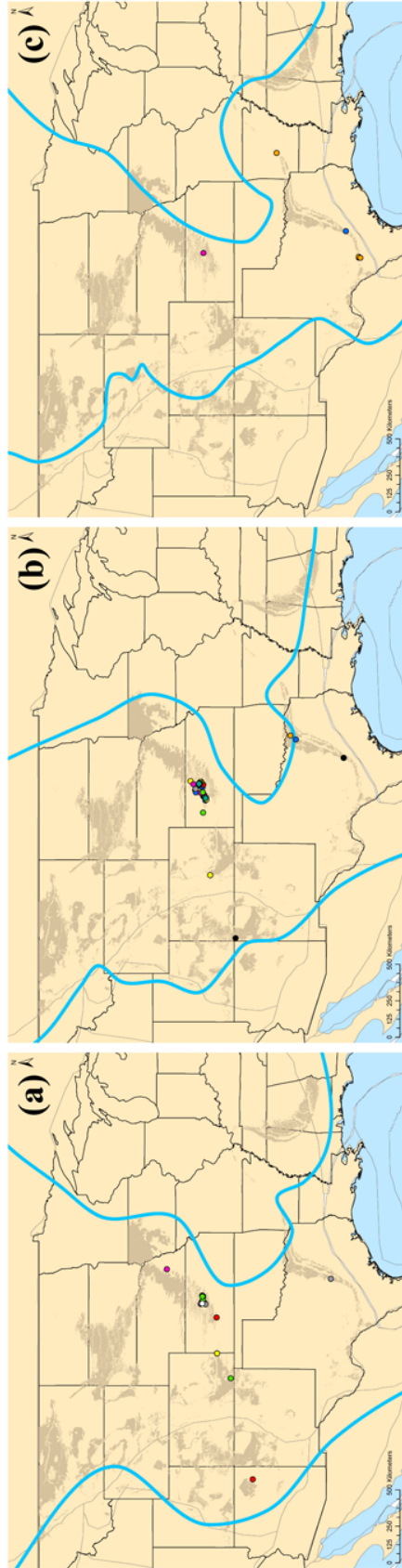
Appendix 1-45. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Ptychodus mortoni* (black) and *Ptychodus whipplei* (white) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



Appendix 1-46. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Pycnodon mortoni* (black) and *Rhinobatos incertus* (light green) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



Appendix 1-47. PaleoGIS (Rothwell Group 2007) range reconstructions illustrating the palaeobiogeographic patterns uncovered for *Pycnodon whipplei* (white) and *Rhinobatos incertus* (light green) during the Late Cretaceous. Late Cretaceous stages: (a) Cenomanian, (b) Turonian, (c) Coniacian, (d) Santonian, (e) Campanian. Present day outcrop of Late Cretaceous sediments is also shown (brown).



Appendix 1-48. PaleoGIS (Rothwell Group 2007) reconstructions showing the approximate boundaries of the WIS and occurrence records during the Late Cretaceous stages: (a) Cenomanian, (b) Coniacian, (c) Maastrichtian. Boundaries of seaway provided with assistance of Richard Mackenzie and Peg Yacobucci. Note that boundaries represent average sea-level at any stage, not necessarily high-stand. Present day outcrop of Late Cretaceous sediments is also shown (brown).

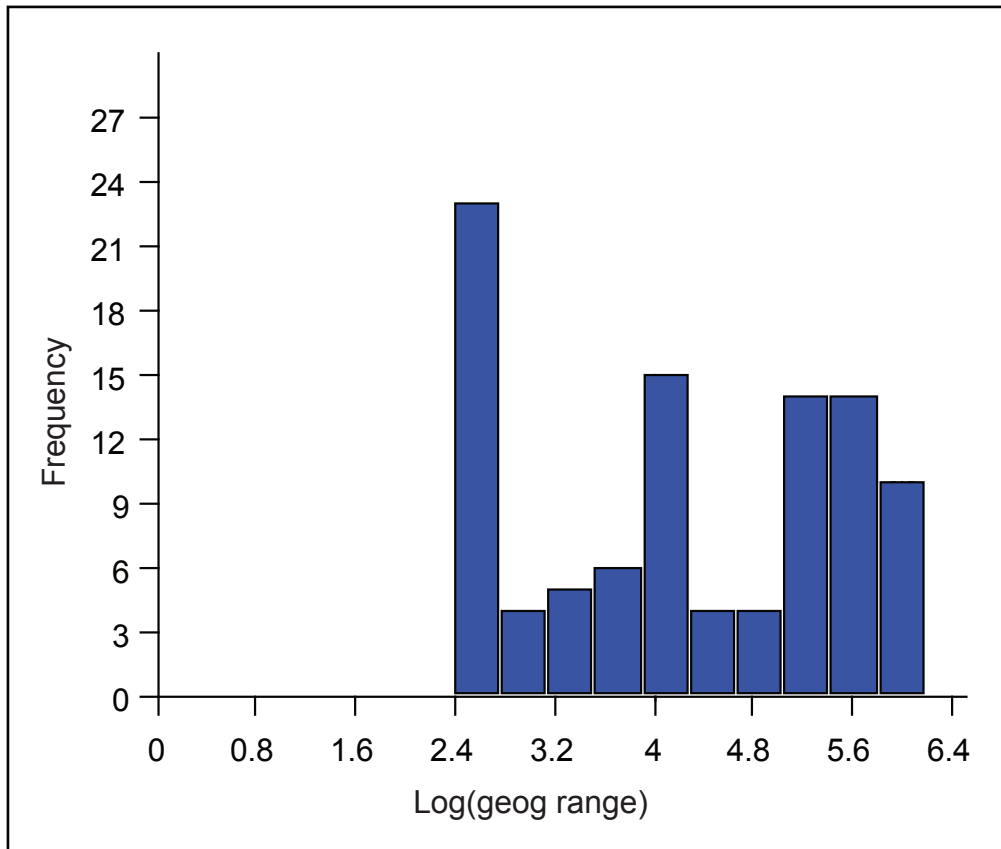
Appendix 2-1. Species range size (reconstructed area and latitudinal extent) and outcrop area during each geologic stage. Coding for survivors and invaders: 1 = survived or invaded in the subsequent stage, 0 = did not survive or invade in the subsequent stage. Abbreviations of geologic stages: CEN = Cenomanian, TUR = Turonian, CON = Coniacian, SAN = Santonian, CAM = Campanian, MAA = Maastrichtian.

Species	Stage	Range Area (km ²)	Latitudinal Extent + 1 (DD)	No. Unique Localities	Survived Into Next Stage	Are Invasive In Next Stage
<i>Exogyra columbella</i>	CEN	805096	12	15	0	0
<i>Exogyra levis</i>	CEN	1085515	16	25	0	0
<i>Exogyra olisiponensis</i>	CEN	10482	2	8	0	0
<i>Exogyra trigeri</i>	CEN	7161	2	5	0	0
<i>Ilmatogyra arietina</i>	CEN	92981	5	10	0	0
<i>Ostrea beloiti</i>	CEN	920545	13	56	1	0
<i>Pseudoperma congesta</i>	CEN	314	1	1	1	1
<i>Pycnodonte newberryi</i>	CEN	266117	8	37	1	0
<i>Sciponoceras gracilis</i>	CEN	1408277	13	58	1	0
<i>Turritella whitei</i>	CEN	10206	4	3	0	0
Outcrop Area	CEN	156313				
<i>Actinocamax manitobensis</i>	TUR	42420	9	4	1	0
<i>Anisomyon apicalis</i>	TUR	504863	13	11	1	0
<i>Anomia cobbani</i>	TUR	9365	3	12	0	0
<i>Anomia pfeiferensis</i>	TUR	5768	2	8	0	0
<i>Anomia subquadrata</i>	TUR	17259	9	2	1	1*
<i>Baculites mariasensis</i>	TUR	242	1	2	1	1
<i>Baculites undulatus</i>	TUR	201070	8	9	0	0
<i>Ostrea beloiti</i>	TUR	314	1	1	0	0
<i>Ostrea malachitensis</i>	TUR	62763	4	7	0	0
<i>Pseudoperma bentonensis</i>	TUR	1086443	12	19	0	0
<i>Pseudoperma congesta</i>	TUR	1266953	12	13	1	0
<i>Pycnodonte</i>	TUR	212743	7	11	0	0

<i>newberryi</i>						
<i>Sciponoceras gracilis</i>	TUR	95402	5	4	0	0
Outcrop Area	TUR	118608				
<i>Actinocamax manitobensis</i>	CON	314	1	1	0	0
<i>Anisomyon apicalis</i>	CON	314	1	1	0	0
<i>Anomia subquadrata</i>	CON	138229	11	7	1	0
<i>Baculites asper</i>	CON	1044159	14	31	1	0
<i>Baculites codyensis</i>	CON	768680	14	49	1	0
<i>Baculites mariasensis</i>	CON	538390	11	26	0	0
<i>Baculites sweetgrassensis</i>	CON	170605	8	4	0	0
<i>Baculites thomi</i>	CON	314	1	1	1	0
<i>Pseudobaculites nodosus</i>	CON	17937	3	4	0	0
<i>Pseudobaculites wyomingensis</i>	CON	16135	2	4	0	0
<i>Pseudoperna congesta</i>	CON	1501675	14	40	1	0
Outcrop Area	CON	119672				
<i>Anomia subquadrata</i>	SAN	10908	8	2	1	0
<i>Baculites aquilaensis</i>	SAN	361	1	2	1	1
<i>Baculites asper</i>	SAN	180962	10	5	0	0
<i>Baculites codyensis</i>	SAN	773196	14	28	1	0
<i>Baculites haresi</i>	SAN	314	1	1	1	1
<i>Baculites thomi</i>	SAN	25782	4	4	1	1
<i>Exogyra laeviuscula</i>	SAN	354	1	2	0	0
<i>Exogyra tigrina</i>	SAN	353	1	2	0	0
<i>Pseudoperna congesta</i>	SAN	512829	12	9	1	0
Outcrop Area	SAN	131090				
<i>Actinosepia canadensis</i>	CAM	9747	2	2	1	1
<i>Agerostrea falcata</i>	CAM	314	1	1	1	1
<i>Anisomyon borealis</i>	CAM	160223	9	4	1	0
<i>Anisomyon centrale</i>	CAM	131853	10	6	1	0
<i>Anomia argentaria</i>	CAM	30773	3	2	1	0
<i>Anomia gryphorhyncus</i>	CAM	314	1	1	1	1
<i>Anomia</i>	CAM	123800	10	6	1	0

<i>micronema</i>						
<i>Anomia obliqua</i>	CAM	2758	2	16	0	0
<i>Anomia subquadrata</i>	CAM	314	1	1	0	0
<i>Baculites aquilaensis</i>	CAM	270748	11	35	0	0
<i>Baculites codyensis</i>	CAM	8742	4	2	0	0
<i>Baculites corrugatus</i>	CAM	186135	8	14	1	0
<i>Baculites crickmayi</i>	CAM	302153	11	13	0	0
<i>Baculites gilberti</i>	CAM	363088	11	28	0	0
<i>Baculites haresi</i>	CAM	411133	12	28	0	0
<i>Baculites rugosus</i>	CAM	418245	11	16	0	0
<i>Baculites taylorensis</i>	CAM	307332	10	7	0	0
<i>Baculites texanus</i>	CAM	6697	1	8	0	0
<i>Baculites thomi</i>	CAM	176083	9	10	0	0
<i>Crassostrea glabra</i>	CAM	14950	7	4	1	0
<i>Drepanochilus evansi</i>	CAM	255	1	3	1	1
<i>Euspira rectilabrum</i>	CAM	314	1	1	1	1
<i>Eutrophoceras alcesence</i>	CAM	57824	4	4	0	0
<i>Eutrophoceras dekayi</i>	CAM	7519	2	6	1	1
<i>Exogyra costata</i>	CAM	13023	3	4	1	0
<i>Exogyra erraticostata</i>	CAM	800	1	5	0	0
<i>Ostrea plumosa</i>	CAM	197716	5	5	0	0
<i>Ostrea russelli</i>	CAM	290689	12	18	1	0
<i>Pseudobaculites natosini</i>	CAM	314	1	1	1	0
<i>Pseudoperma congesta</i>	CAM	490088	11	13	1	0
<i>Pycnodonte mutabilis</i>	CAM	616	1	3	0	0
<i>Turritella vertebroides</i>	CAM	557	1	2	0	0
<i>Tusoteuthis longa</i>	CAM	2822	1	7	0	0
Outcrop Area	CAM	253068				
<i>Actinosepia canadensis</i>	MAA	191574	11	23	NA	NA
<i>Agerostrea falcata</i>	MAA	28664	10	2	NA	NA
<i>Anisomyon</i>	MAA	314	1	1	NA	NA

<i>borealis</i>						
<i>Anisomyon centrale</i>	MAA	314	1	1	NA	NA
<i>Anomia argentaria</i>	MAA	314	1	1	NA	NA
<i>Anomia gryphorhyncus</i>	MAA	118068	7	20	NA	NA
<i>Anomia micronema</i>	MAA	3328	2	4	NA	NA
<i>Baculites corrugatus</i>	MAA	314	1	1	NA	NA
<i>Baculites larsoni</i>	MAA	16630	4	11	NA	NA
<i>Belemnitella bulbosa</i>	MAA	9720	2	18	NA	NA
<i>Crassostrea glabra</i>	MAA	368355	7	12	NA	NA
<i>Drepanochilus evansi</i>	MAA	185039	7	39	NA	NA
<i>Eubaculites carinatus</i>	MAA	2712	2	3	NA	NA
<i>Euspira obliqua</i>	MAA	2036	2	5	NA	NA
<i>Euspira rectilabrum</i>	MAA	1297	2	2	NA	NA
<i>Eutrophoceras dekayi</i>	MAA	363784	13	7	NA	NA
<i>Exogyra costata</i>	MAA	13932	2	3	NA	NA
<i>Graphidula culbertsoni</i>	MAA	6255	2	30	NA	NA
<i>Ostrea russelli</i>	MAA	314	1	1	NA	NA
<i>Ostrea translucida</i>	MAA	10122	2	18	NA	NA
<i>Pseudobaculites natosini</i>	MAA	314	1	1	NA	NA
<i>Pseudoperna congesta</i>	MAA	2215	2	2	NA	NA
<i>Trachybaculites columna</i>	MAA	1054	1	8	NA	NA
Outcrop Area	MAA	128195				



Appendix 2-2. Histogram of Log(geographic range) for all reconstructed ranges of molluscan taxa during the Late Cretaceous.

APPENDIX 3. References used to correlate Late Cretaceous fossil-bearing strata of the Western Interior Seaway and Gulf Coast. Correlation results are presented in Table 4.

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